VARIATION AND INHERITANCE IN ABNORMALITIES OCCURRING AFTER CONJUGATION IN PARAMECIUM CAUDATUM

DISSERTATION

SUBMITTED TO THE BOARD OF

UNIVERSITY STUDIES

OF

THE JOHNS HOPKINS UNIVERSITY

IN CONFORMITY WITH THE REQUIREMENTS

FOR THE DEGREE

OF

DOCTOR OF PHILOSOPHY

BY

RUTH JENNINGS STOCKING

BALTIMORE
1915

Diss.
Baltimore
1915

75453

INHERITANCE AND VARIATION IN ABNORMALITIES OCCURRING AFTER CONJUGATION IN PARAMECIUM CAUDATUM

DISSERTATION

SUBMITTED TO THE BOARD OF

UNIVERSITY STUDIES

OF

THE JOHNS HOPKINS UNIVERSITY

IN CONFORMITY WITH THE REQUIREMENTS

FOR THE DEGREE

OF

DOCTOR OF PHILOSOPHY

R. UNIV.
BIBLIOTHEEK
LEIDEN

BY

RUTH JENNINGS STOCKING

BALTIMORE
1915

Reprinted from THE JOURNAL OF EXPERIMENTAL ZOÖLOGY, Vol. 19, No. 4
November, 1915

VARIATION AND INHERITANCE IN ABNORMALITIES OCCURRING AFTER CONJUGATION IN PARAMECIUM CAUDATUM

RUTH J. STOCKING

From the Zoölogical Laboratory of the Johns Hopkins University[1]

TWENTY FIGURES

CONTENTS

I. Introduction 387
II. Methods 390
III. Experimental Cultures 391
IV. Types of Abnormal Races 397
V. Nature of the Abnormalities 407
VI. The Abnormalities as Hereditary Characters:
Variation, Inheritance, and Selection 412
Experiments in Selection 414
Relation to Biparental Inheritance 440
VII. Summary and Discussion of Results 444
VIII. Literature 449

I. INTRODUCTION

The fact that there are two kinds of teratological variation, one caused by gametic constitution and therefore heritable, the other occasioned by the action of environmental conditions, and not heritable, has been recognized for some years. There was for a time an endeavor on the part of many investigators to show that all abnormalities were due to conditions of nurture; but the discovery of the strict mendelian inheritance of a large number of malformations has overthrown that theory. In many of the metazoa both kinds of teratological variation, gametic and environmental, have been studied, and their causes and behavior partly determined. In the protozoa the abnormalities caused by the action of external factors have received by far the great-

[1] Part of the work here reported was completed while the author held the Alice Freeman Palmer Research Fellowship of Wellesley College.

est amount of attention, heritable abnormalities having been but little studied. This paper presents an investigation of heritable abnormalities in Paramecium.

The principal points examined in this presentation are the following: The origin and nature of the abnormalities; their relation to conjugation; their inheritance and variation in uniparental reproduction, with relation to the present day problems of 'pure line' work; how precisely inheritance occurs; whether there are variations of kind and degree of abnormality; whether such variations are themselves inherited; whether by selection abnormal stocks multiplying asexually can be altered in their hereditary characteristics or differentiated into two or more hereditarily diverse stocks; their relation to biparental inheritance; their relation to survival.

Previous work on the abnormalities found in protozoa has dealt mainly, as before remarked, with the results of environmental action. Jollos ('13) subjected a race of Paramecium caudatum to changes of temperature and obtained by this method differences in size, as did Hertwig ('08), Popoff ('08, '09), and Rautman ('09). Jollos found that these changes are transitory and soon disappear as the paramecia become adapted to their new conditions. In a short preliminary note, which does not present the evidence for his conclusions, he states that in one case he obtained a permanent change. He subjected a race of Paramecium to a high temperature and obtained a race which was permanently small at high, normal, and low temperatures. Popoff ('09) was able to produce by experimental means two abnormal races of Stentor, one giant and the other dwarf. He centrifuged a dividing Stentor, and so caused an unequal distribution of the nuclear material. The daughter cell which received the smaller part was one-fourth the size of the cell which received the larger part. These two multiplied normally for about a week and during that time retained their abnormal sizes. The cultures were then lost. He obtained another giant race of Stentor by suddenly cooling a dividing individual. The division did not take place and the animal reorganized into a single individual which grew and subsequently

divided, forming a giant race which was kept for about forty-five days, and during that time bred true. Lewin ('10) obtained abnormally-nucleate races of Paramecium by cutting an individual through the macronucleus. The production of form abnormalities in Paramecium by cutting and other experimental means has been studied by Calkins ('11), Peebles ('12), Balbiani ('93), McClendon ('09), and Jennings ('08). They all found that such experimentally produced abnormalities are mechanically handed on to one daughter cell at each division for a longer or shorter time. But such abnormal forms are gradually remodelled during successive generations, or die, and their normal sisters show no tendency to produce abnormal progeny. The teratological variations that arise spontaneously in a culture multiplying vegetatively have been studied extensively by Jennings ('08). With one exception he found that all such forms either die very soon or give rise to a race of normals. In one case he did find that the abnormal individual gave rise to a race of abnormals, the deformity being such as to prevent the daughter cells from separating after division, thus forming what have been called 'double monsters.' In all other cases the abnormality was not a race character but an individual character and was not inherited. During the course of a year's work at the Johns Hopkins University I followed the history of several abnormal forms which had arisen in the cultures of normals being carried on by other workers in the laboratory. In no case did these forms give rise to a race of abnormals; in one case a race of normals resulted; in all other cases death occurred either before any divisions had taken place or after one or two irregular divisions. In rare cases, Jennings ('13) found, abnormalities may arise in the members of split pairs; that is, in the members of pairs separated before conjugation has been completed. But these also never gave rise to a race of abnormals, either dying very soon or becoming entirely normal.

Teratological variations arising soon after conjugation have been described in a few cases. Simpson ('01) observed four daughter cells of a normal exconjugant Paramecium, three of which were normal while the fourth was posteriorly split. This

animal divided eight times and its history was similar to that given above for the experimentally produced abnormalities in Paramecium. The abnormal character was handed on to one cell at each division, and the abnormal animal produced by the eighth division died. All of the sister cells and their progeny were normal. The only other observation known to me on the abnormalities arising after conjugation is made by Jennings in his 1913 paper quoted above. While he found only extremely rare and transitory abnormalities among his 'split pairs' and 'free' individuals, he found a large proportion of malformations among his exconjugants and their progeny. He describes their different types, characteristics, and constant and continued appearance throughout the course of his experiments; and adds, "A precise study is greatly needed, as to the minute characteristics of these abnormalities, their heritability, their experimental cause, and their cytological basis." It was at his suggestion that a series of experiments was started for the purpose of studying these problems, and under his direction that these experiments have been carried through. I wish to express here my most sincere thanks for the constant help he has given during the entire course of the work.

II. METHODS

In all of the cultures on which this work is based the method of handling, cultivating, and recording was identical with that described by Jennings ('13). Conjugation was first induced; after the pairs had separated the two members were isolated and cultivated separately in $\frac{1}{16}$ per cent Horlick's malted milk (Peebles, '12). Each pair was numbered, and the two members of a pair designated *a* and *b*; the races which arose from these exconjugants were called after them in the same way, *2a*, *2b*, *3a*, and so on. Beside the slide cultures, mass cultures were also kept for each race. These were kept in bottles and each bottle was labelled correspondingly, *2a*, *2b*, *3a*, and so on. The method of recording described by Jennings was supplemented in my work by drawings of the abnormal forms. In a few cases

this was impossible because of the rapid movements of the animal. For about two weeks after conjugation camera lucida drawings were made of the abnormal forms. These were often less active than the normal forms and after being in the same drop of culture fluid for two days all of the individuals were more or less sluggish. So with a little patience camera lucida drawings could be obtained of almost all the abnormals. When the number to be examined and drawn became very large, however, there was no time for that procedure and free hand drawings were made in the majority of cases, camera lucida only in such cases as seemed of more than ordinary interest. The slide cultures were examined every other day during the cool weather, every day when it became very warm, the individuals counted, the abnormals drawn, selection made of those by which the slide cultures should be carried on, and the others put into the bottle mass-culture corresponding to that race. The individuals selected for slide culture were then washed in the milk solution, and put into fresh fluid on clean slides.

III. EXPERIMENTAL CULTURES

The material presented in this paper is derived from three experimental cultures carried from the fall of 1912 to the spring of 1914. The first experiment, conducted from December 2, 1912, to June 11, 1913, was carried out with exconjugant members of a wild population which doubtless included members of many diverse stocks. The chief aim of this first experiment was to ascertain whether or not abnormalities were ever inherited, and to what extent. From November 25, 1913 to December 22, 1913, a second experiment was conducted on a group of animals all descended from one individual, constituting therefore a 'pure line' or 'clone.' It was concerned mainly with determining the effect of conjugation among the members of a single clone, particularly as to the production of abnormalities; this was brought out by a comparison of exconjugants with members of split pairs belonging to the same clone. In the first experiment some work on the effect of selection was attempted; but the third experiment, carried out on a wild population from

January 14, 1914, to April 1, 1914, was concerned wholly with that problem. In it an attempt was made to ascertain the efficacy of selection as a means of breaking a single clone into two or more lines differing hereditarily in amount or kind of abnormality.

In all three of the experiments, in two of which very large numbers of exconjugants and their descendants were studied, a large proportion of the resulting races were abnormal, just as was the case in the exconjugants studied by Jennings ('13). In Experiment 1, with a wild population, the proportion of abnormals was 36 per cent of the entire 262 exconjugants. In Experiment 2, with the members of a clone, the proportion of abnormals was much higher, being 81 per cent of the whole 200. In Experiment 3 the number of exconjugants studied was small; the abnormal races formed 43 per cent of the total 28. In the 54 members of the 27 split pairs of Experiment 2, twenty of which were cultivated for 19 days, and thirty-four for 7 days, no abnormals at all appeared. Whenever sets of individuals are isolated without conjugation and cultivated in the same way, no such proportion of abnormals are observed; indeed as a rule no abnormals whatever are obtained. We shall return later to the relation of the abnormalities to conjugation (page 412).

The exconjugants from large cultures of paramecia may be divided, on the basis of their subsequent history, into a number of diverse classes, which are summarized for our three cultures in table 1. 1) A few pairs, in some cultures, never separate, but die while united. 2) A considerable number, in some cases, die within 24 hours after separation. 3) Others live after separation—often for a long time—but never divide. 4) A fourth group divide, but produce individuals that are in some way and to some degree abnormal. 5) Finally, a certain proportion propagate normally after conjugation, giving rise to typical progeny. The proportions of these different classes are shown in table 1.

The single pair that did not separate lived united for five days. The exconjugants that never divide after separation form a large proportion of the abnormal individuals, rising to 28 per cent of

TABLE 1

Diverse types of exconjugants, their number and proportion in the three experimental cultures

EXPERIMENT	1) NEVER SEPARATED		2) DIED FIRST DAY		3) NEVER DIVIDED		4) PROGENY ABNORMAL		5) PROGENY NORMAL		TOTAL
	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	
1	0		25	10.0	74	28.0	21	8.0	142	54.0	262
2	2	1.0	3	1.5	27	14.0	133	66.0	35	17.5	200
3	0		0		0		12	43.0	16	57.0	28
Total.	2	0.4	28	5.7	101	20.6	166	33.9	193	39.4	490

all in Experiment 1. These often live for some time, the length of life varying greatly. The length of life in days for the 101 exconjugants that never divided was as follows:

Length of life in days	1	3	5	7	9	11	13	15	17	Total
Number of exconjugants:										
Experiment 1	0	0	46	10	4	5	5	3	1	74
Experiment 2	2	8	4	2	1	10	0	0	0	27
Total	2	8	50	12	5	15	5	3	1	101

All of the animals of Experiment 2 which never divided were dead by the thirteenth day after conjugation; in Experiment 1 nine such individuals lived for some time after this. Those that live for a number of days often change a great deal in size and shape; many of them become immensely large. Twenty-eight of these individuals were measured; for their lengths and diameters on successive days after conjugation see p. 474.

The diversities of size and shape among these individuals is illustrated in figure 1, which shows nine of the individuals of Experiment 1 which never divided, all camera lucida drawings to the same scale. The usual size of Paramecium caudatum on the same scale is shown in figure 5.

The largest single individual Paramecium that I have ever seen was the first individual listed below for Experiment 1; it measured 520 by 150 microns, as against a usual length of 150 to 200 microns. The smallest individual that never divided was likewise in Experiment 1; it measured 128 by 10 microns. It is evident that there was much greater variability in size, shape,

and length of life, in these individuals of Experiment 1, than in those of Experiment 2. It appears probable that this is con-

Experiment 1

MEASUREMENTS ON				
Seventh day	Ninth day	Eleventh day	Thirteenth day	Fifteenth day
520 x 150	340 x 130	320 x 100	220 x 55	
450 x 120		420 x 150		
420 x 92	260 x 80			
400 x 140		420 x 120		220 x 90
400 x 135	390 x 160			
350 x 110				
350 x 80				
340 x 110		350 x 130		
340 x 100				
340 x 70			220 x 105	
330 x 100		240 x 150		
300 x 120				
290 x 140			240 x 105	
290 x 100		300 x 170		
280 x 140				
210 x 115				
200 x 20		210 x 20		
190 x 160				
165 x 20	250 x 50			
129 x 10	200 x 35	250 x 60		
Ave. 315 x 102	288 x 91	314 x 112	227 x 88	220 x 90

Experiment 2

MEASUREMENTS ON		
Third day	Fifth day	Seventh day
240 x 75		
240 x 55		
215 x 35		
210 x 65		
195 x 55	145 x 35	150 x 20
190 x 45		
175 x 35		
	145 x 35	
Ave. 209 x 52.....	145 x 35	150 x 20

nected with the fact that the former culture consisted of wild individuals, probably of diverse stocks, while the latter consisted of members of a single clone. This matter will be taken up later.

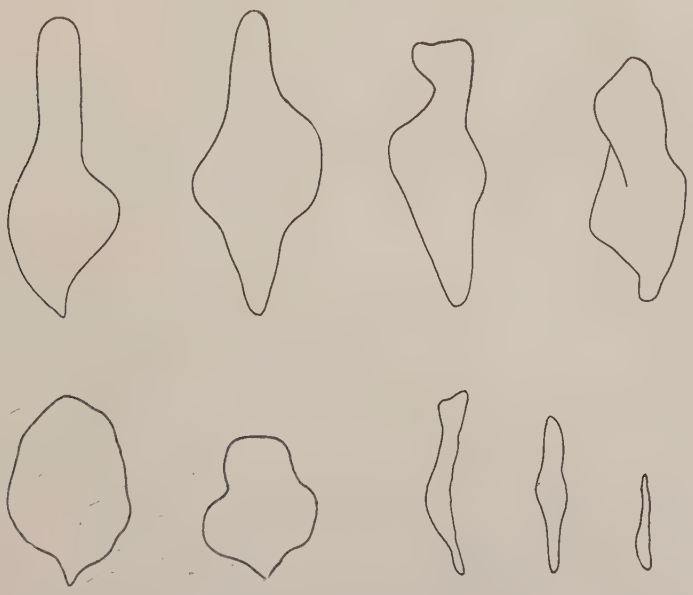


Fig. 1 Nine of the individuals of Experiment 1 which never divided, showing the diversity of form and size among this class. In this figure and in figures 2, 3, and 4, the animals were all drawn by means of the camera lucida, and are all to the same scale. (× 100)

As a rule there appeared to be a tendency for these large individuals to gradually decrease in size (as shown by the measurements above given). Figures 2, 3, and 4 show the changes in form and size in certain cases. The forms were frequently nearly normal; sometimes very abnormal, as the figures show. These individuals that never divided were usually black and granular, and often changed shape when transferred to fresh culture fluid, becoming swollen at the anterior end; they later resumed their original form. A cytological study of these animals might be of interest in connection with the 'Kern-Plasm Relation' theory, and with the mechanics of division. Such

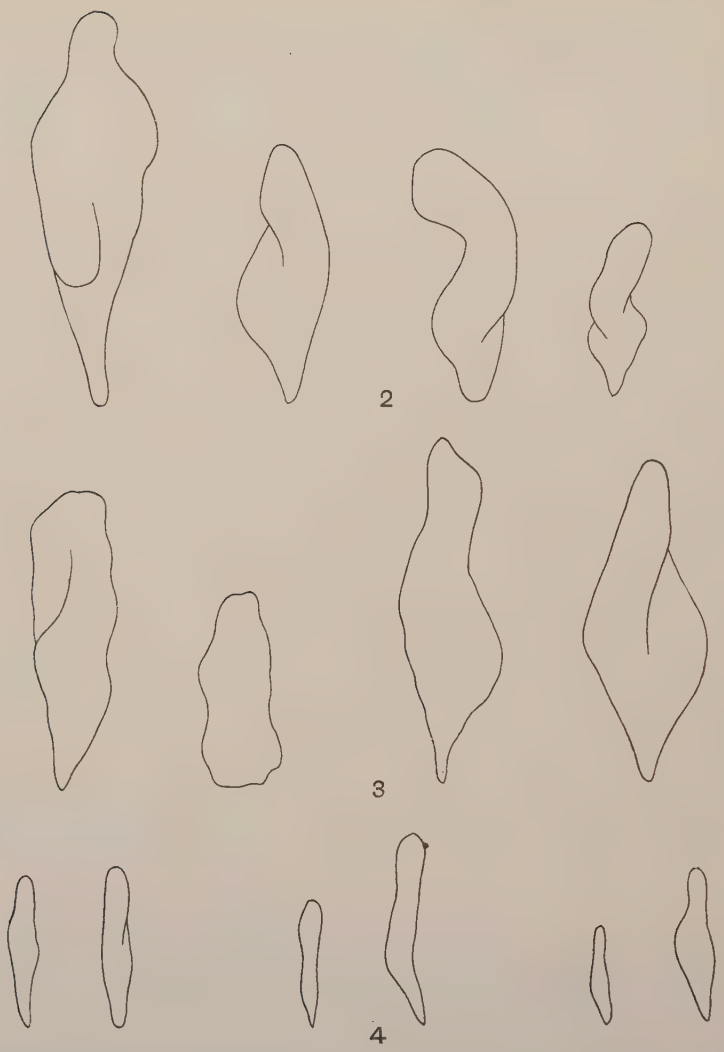


Fig. 2 One of the individuals (15a) of Experiment 1 which never divided, showing the decrease of size and change of form it underwent from December 9 to December 15, inclusive. (× 100)

Fig. 3 Two of the individuals of Experiment 1 which never divided, showing the changes of form and size they underwent. The two figures at the left show *16a* on December 9 and 11; the other two figures show *110a* on December 9 and 13. (× 100)

Fig. 4 Three of the individuals of Experiment 1 which never divided The first two figures show *52a* on December 9 and 13; the second two figures show *89b* on December 9 and 13; the last two, *19b* on December 9 and 11. (× 100)

large individuals, never dividing, do not appear after conjugation in all cultures; some later attempts to obtain them for study have not been successful.

IV. TYPES OF ABNORMAL RACES

Of chief interest for our purposes are the exconjugants which divided, but produced progeny some of which were deformed. The lines of descent to which these deformed individuals belong I shall call abnormal lines or races; it is they that provide the material for the study of heredity, variation, and selection here set forth.

The abnormal lines differ greatly in the proportion of abnormal individuals produced and in their later history. Not all the individuals produced are abnormal; and not all the abnormal races remain abnormal indefinitely. Reserving many of the details for our section on the results of selection, we may divide these abnormal races into three classes:

1. In the first class are those races which ultimately became normal. There were 39 races of this class. The proportion of abnormal individuals produced ranges in the different races from one per cent to 41 per cent. In these races the abnormal individuals gradually disappear, till finally only normals are produced. Some of the abnormals of this class may be compared with the experimentally deformed animals; and with those which arise rarely in cultures that have not conjugated. They always form a very small proportion of their race, and either die out or produce normal daughter cells. Others however are not strictly comparable with the transient abnormalities described by other workers. They form a considerable and constant proportion of the individuals of their race; are continually produced for several generations; and are often descended from both normal and abnormal sister cells. But through the action of natural conditions and in some cases the selection of the normal individuals, the abnormals become gradually eliminated and the race entirely normal. Data on these 39 races of the three experiments is given in table 2.

TABLE 2

The 39 abnormal races which became entirely normal

EXPERIMENT	RACE	LENGTH OF LIFE IN DAYS	NUMBER OF GENERATIONS	NUMBER OF NORMALS	NUMBER OF ABNORMALS	PER CENT ABNORMAL
1	96a	15	10	314	3	1
	35a	17	10	32	1	3
	14a	13	11	38	3	7
	102a	15	7	17	3	15
	63a	15	7	13	5	28
2	84b	9	5	16	1	6
	49b	9	5	14	1	7
	53a	11	6	25	2	7
	32a	11	8	35	4	10
	63b	11	6	45	6	12
	34a	11	6	14	2	13
	57a	11	5	14	2	13
	29a	11	9	33	5	13
	50b	11	5	12	2	14
	30a	11	7	39	7	15
	40a	9	4	10	2	17
	15a	11	7	17	4	19
	73a	11	9	17	4	19
	56a	11	9	57	13	19
	47a	11	5	16	4	20
	57b	11	9	31	8	21
	92b	22	7	28	8	22
	88a	13	6	13	4	23
	35b	11	8	47	15	24
	12b	11	3	3	1	25
	26a	9	3	3	1	25
	34b	11	4	9	3	25
	54a	11	5	10	4	29
	55b	9	4	10	4	29
	95b	11	3	9	4	31
	99b	9	2	2	1	33
	55a	15	3	4	2	33
	96b	9	4	10	5	33
	85b	9	3	7	4	36
	38a	11	4	10	6	38
	59b	13	7	9	6	40
	16b	15	6	16	11	41
3	52b	17	9	250	2	1
	53b	21	8	212	7	3
Range...		9 to 22	2 to 11	2 to 314	1 to 15	1 to 41
Average.		12	6	38	4	10

Figures 5 and 6 give pedigrees of two of these transiently abnormal races, numbers 14a and 102a, which are fairly typical of this group. Race 14a (fig. 5) was kept for thirteen days. During that time it divided 17 times, giving an average of 1.13 divisions a day. It showed no abnormalities until December 11 (nine days after conjugation), when the three individuals which had arisen from the apparently normal animals selected on December 9 were, one large and very abnormal, one small and abnormal, and the third small and almost normal in appearance. The large one died after having divided once. The two small ones had divided to form four normal individuals on December 13, and on December 15 had given rise to eight perfectly normal animals which were then discarded.

Race 102a (fig. 6) divided very slowly at first, averaging 0.5 divisions a day. The average division a day for the whole time the race was kept was 0.8, the animals dividing much more rapidly toward the last. This exconjugant showed no signs of being abnormal until December 11, when the three forms present were very abnormal, two being doubles and one a very much swollen individual. One of the double forms moved in a circle so swiftly that it could not be drawn. Both of the double forms died without dividing; the large swollen one gave rise to a perfectly normal race which was discarded on December 17.

2. In the second class of abnormal races are those which persistently produced abnormal individuals throughout their history. There were 9 such races in Experiment 1 and 88 in Experiment 2. They differed greatly in the proportions of abnormals produced, varying from races 100 per cent abnormal to those but 3 per cent abnormal. The pertinent data for these 97 persistently abnormal races is given in table 3.

In many of these persistently abnormal races individuals appeared which were normal in form. But these if propagated eventually produced abnormals. Further details as to this will be given in our section on the effects of selection.

Figures 7 and 8 give pedigrees of two of the short-lived races of this group, 39b and 40b, which show the typically persistent

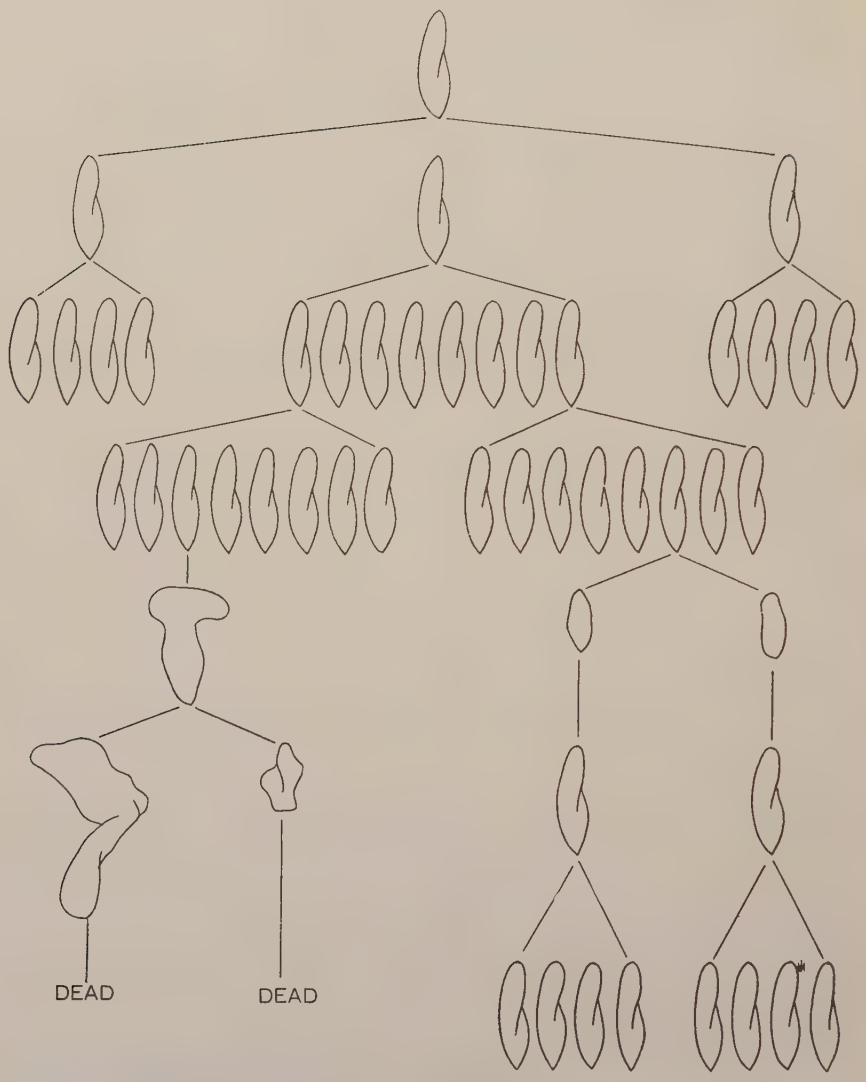


Fig. 5 Pedigree of *14a*, one of the abnormal races which became entirely normal. (× 100)

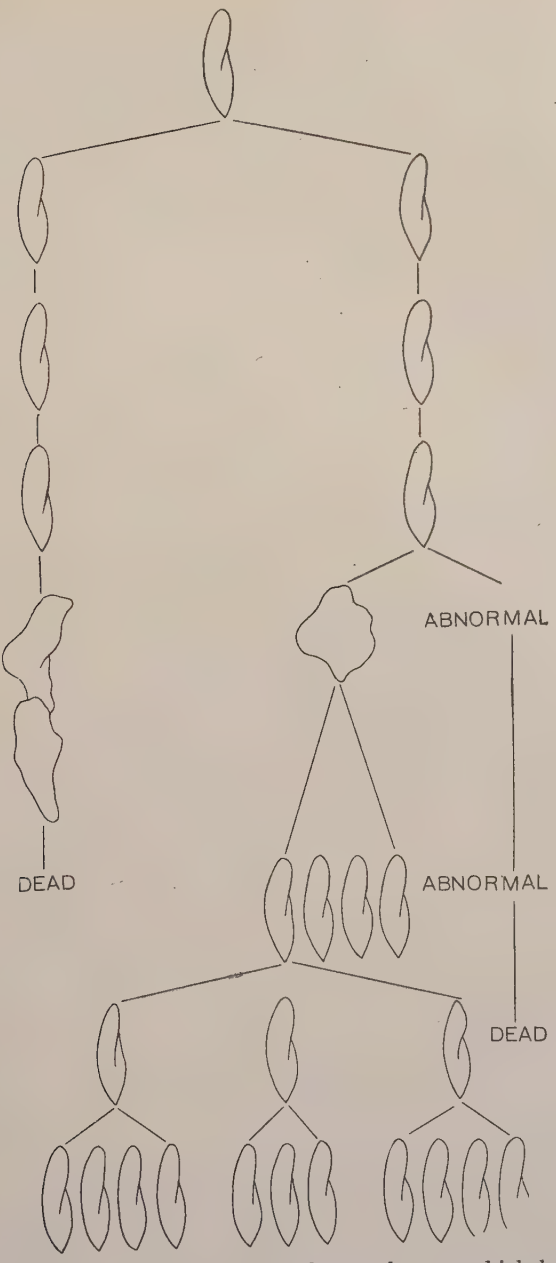


Fig. 6 Pedigree of *102a*, one of the abnormal races which became entirely normal. On some dates the abnormal forms could not be drawn; they are simply designated as 'abnormal.'

TABLE 3

The 97 races which remained persistently abnormal

EXPERIMENT	RACE	LENGTH OF LIFE IN DAYS	NUMBER OF GENERATIONS	NUMBER OF NORMALS	NUMBER OF ABNORMALS	PER CENT ABNORMAL
1	2a	15	3	3	1	25
	16b	9	5	18	2	10
	25b	9	2	0	2	100
	39b	25	9	14	12	46
	40b	17	8	10	8	44
	47a	9	3	0	5	100
	91a	15	2	0	2	100
	106a	9	2	0	2	100
	C	191	303	2027	2683	57
2	2b	27	11	55	19	26
	6a	11	4	5	4	44
	7b	15	6	4	9	69
	8a	17	5	6	7	54
	66b	11	6	4	13	76
	8b	17	7	20	15	43
	9a	11	4	2	6	75
	99b	11	2	2	11	33
	11a	21	10	13	28	68
	11b	21	8	21	14	40
	14b	15	6	17	8	32
	16a	23	7	25	8	24
	18b	11	6	18	5	22
	19a	17	6	21	16	43
	19b	23	6	10	16	66
	20a	27	19	224	187	45
	20b	19	5	11	10	48
	21a	21	10	25	17	40
	21b	13	4	2	5	71
	22a	13	4	6	3	33
	22b	11	4	6	6	50
	23a	25	8	21	5	19
	23b	25	8	33	25	43
	24a	9	2	2	1	33
	24b	11	6	10	4	29
	25a	23	7	13	10	43
	25b	11	4	7	4	36
	27a	11	4	4	5	56
	27b	27	27	303	556	65
	28a	15	5	19	9	32
	28b	13	4	7	8	53
	29b	19	8	26	18	41

TABLE 3—Continued

EXPERIMENT	RACE	LENGTH OF LIFE IN DAYS	NUMBER OF GENERATIONS	NUMBER OF NORMALS	NUMBER OF ABNORMALS	PER CENT ABNORMAL
	30b	19	8	18	17	49
	31a	13	5	5	11	69
	31b	11	5	13	8	38
	32b	11	2	3	1	25
	33a	21	5	12	5	29
	33b	11	5	5	6	55
	35a	11	5	4	11	73
	39a	13	4	3	4	57
	39b	23	8	36	20	36
	43a	27	10	322	22	41
	43b	11	5	13	6	32
	44a	11	4	8	2	20
	44b	13	2	2	2	50
	46b	11	4	11	5	31
	48a	27	19	91	133	59
	48b	23	7	28	9	24
	54b	13	7	27	3	10
	56b	9	4	4	8	66
	58a	17	8	35	4	10
	58b	11	3	3	4	57
	59a	11	6	30	1	3
	61a	13	5	25	7	22
	62b	11	4	4	6	60
	63a	11	5	22	12	35
	65a	17	6	10	9	47
	67a	13	4	11	6	35
	67b	21	6	15	11	42
	68a	19	7	31	4	11
	68b	11	2	4	1	20
	69b	17	8	24	11	31
	70a	21	7	23	41	64
	70b	27	4	18	19	51
	71a	13	5	8	7	47
	72a	15	7	20	10	33
	73b	11	5	7	10	59
	74a	17	7	12	32	73
	74b	11	6	6	26	81
	75a	11	3	5	3	37
	75b	11	5	13	4	24
	76a	11	4	9	8	47
	76b	13	4	9	2	18
	79a	27	21	186	143	43
	82a	9	3	3	6	67

TABLE 3—Continued

EXPERIMENT	RACE	LENGTH OF LIFE IN DAYS	NUMBER OF GENERATIONS	NUMBER OF NORMALS	NUMBER OF ABNORMALS	PER CENT ABNORMAL
2	82b	9	4	4	8	67
	84a	27	7	15	20	57
	89a	11	5	10	66	37
	89b	27	7	45	22	33
	90a	19	4	11	4	27
	90b	21	4	8	4	33
	92a	17	3	7	5	42
	94a	23	7	12	23	66
	94b	13	3	7	5	42
	96a	23	7	18	25	58
	98a	15	5	8	2	20
	99a	13	4	5	3	37
	100b	19	3	6	5	45
Range...		9 to 191	2 to 303	0 to 2027	1 to 2683	3 to 100
Average.		18	9	41	47	53

appearance of the character in all their lines. Race 39b (fig. 7) divided seven times in eight days, forming only normal individuals until December 11, when six of the eight individuals present were very much misshapen. After this date only abnormals were produced by this race, which died out on December 27. There was a very large proportion of double forms among the individuals of this race, eleven of the twenty-five abnormals produced being of this character.

Race 40b (fig. 8) divided regularly to form only normals up to December 11, when three out of the five then present were abnormal. The two normals died out and the race was carried on through the abnormal individuals. These produced only abnormal progeny and the race died out on December 19.

Race C, described on pages 414 to 420, is a typical long-lived race of this group.

3. As the third group of abnormal races we may distinguish those which did not become entirely normal, but from which normal races were obtained by continued selection. This group will be dealt with in our section on selection.

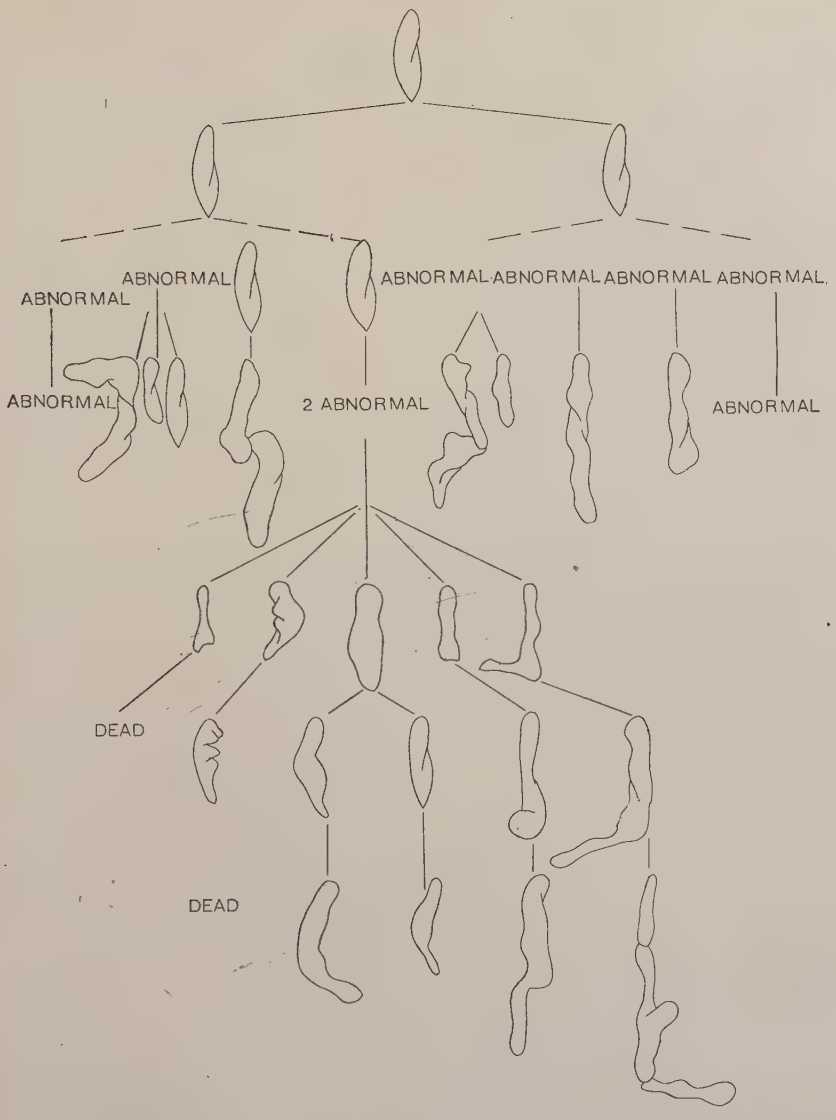


Fig. 7 Part of the pedigree of *39b*, one of the short-lived races which remained abnormal throughout its life. The broken connecting lines designate the omission at that point of two entirely normal generations.

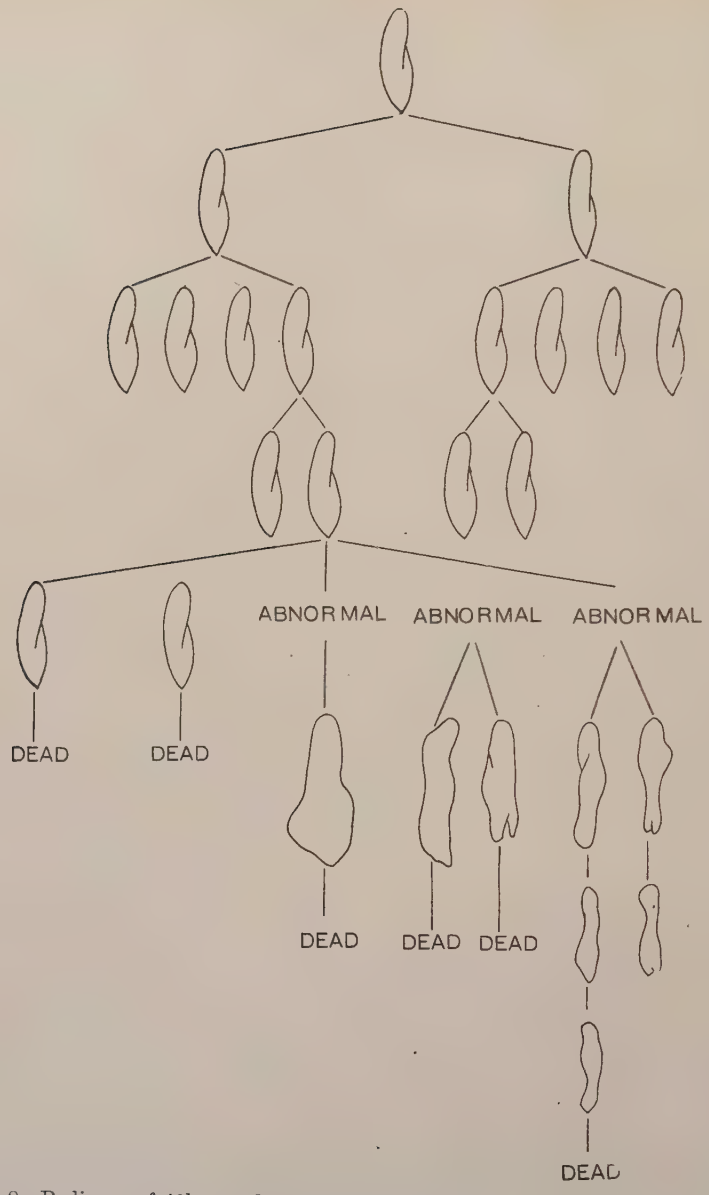


Fig. 8 Pedigree of *40b*, another short-lived race which was abnormal throughout its life.

V. NATURE OF THE ABNORMALITIES

Descriptively considered, the abnormalities shown by the individuals of the abnormal races are of many diverse sorts. I have been able to distinguish 40 different types of abnormals. These are shown in figure 9, and their frequencies in the three experiments are given in table 4. Most of the races of Experiment 1 developed one or more representatives of a large number of these types; some of the races had representatives of all but two or three. The high frequencies of so many of these types in Experiment 1, as given in table 4 shows how great the diversity of form is among the individuals of that group. In experimentally produced abnormalities reported by other workers on other animals, this diversity of type is always shown; as Mall ('08) says, there is never found any precise type of abnormality characteristic of certain conditions, but only a general character, a tendency to abnormality of many different types. But some races of my experiments were more or less characterized by a few types, which I have called their predominant types. The best examples of this predominance of type are race C of Experiment 1, and races 56a, 56b, and 59b of Experiment 3. During the early part of their histories these races showed considerable diversity of abnormal type; but this diversity was rapidly reduced and the abnormals became limited to a few types in all four of these races. During its whole history race C produced in its observed cultures 2683 abnormals; 1331 or 50 per cent of these were of type 33; 945 or 35 per cent were of type 27. The predominant type of the other three races was the same, number 27 of figure 9. Race 56a produced 1428 abnormals; 79 per cent of them were of that type; 59 per cent of the 780 abnormals of 56b were of type 27; and 50 per cent of the 2096 abnormals of race 59b were of the same type.

In the abnormals of Experiment 2 there was considerably less diversity of type than in the abnormals of Experiment 1. Only 30 of the different types were observed in Experiment 2; most of these appeared only a small number of times, 90 per cent of the abnormals being of five types (11, 26, 27, 28, 30). Table 4 gives

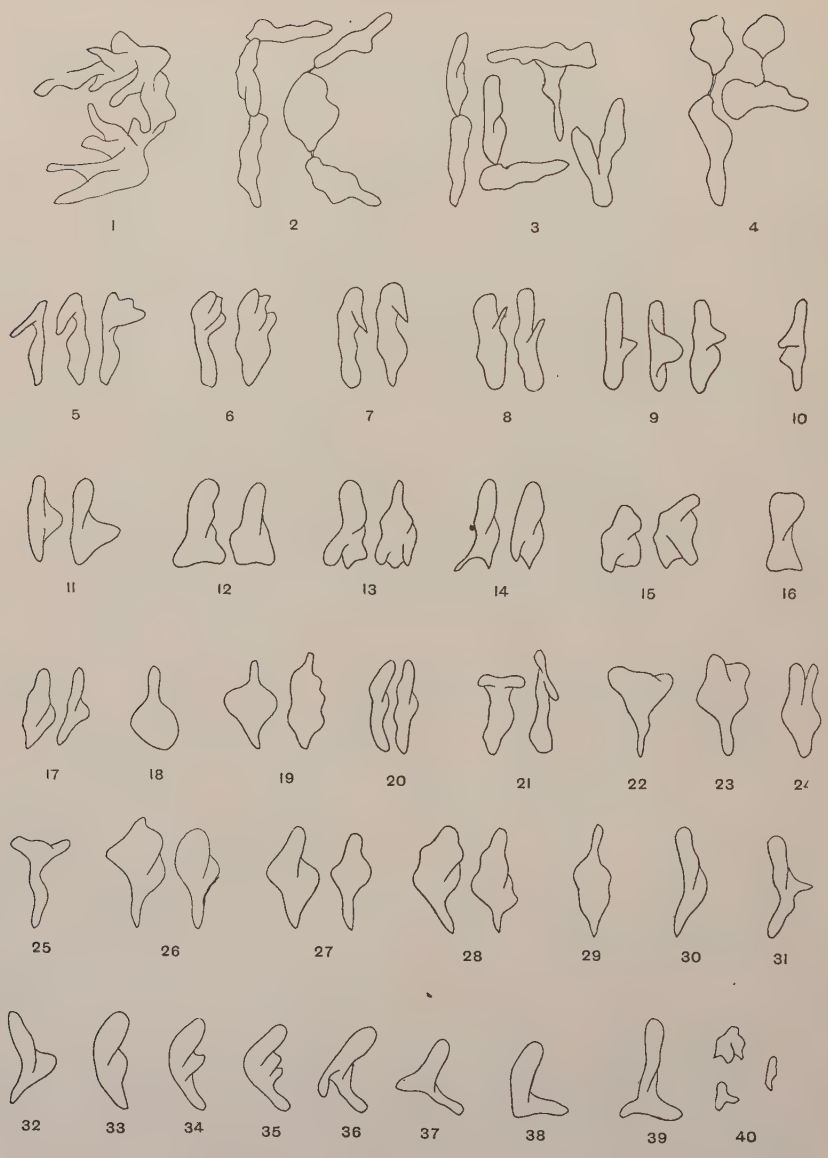


Fig. 9 The 40 types of abnormals observed in the three experiments. In some cases two or more examples of one type are given in order to convey some idea of the variation within a type. The types which appeared in the three experiments and their number and proportion are given in table 4.

the numbers of the thirty types that appeared among the abnormals of this experiment and their frequencies.

Likewise in the abnormals of Experiment 3 there was less diversity of type than in those of Experiment 1. Table 4 gives the numbers of the 27 types observed and their frequencies; 91 per cent of all the abnormals of Experiment 3 were of five types (22, 26, 27, 30, 39).

The lessened diversity of type observed in the experiment with the members of a pure line (Experiment 2) as compared with the members of a wild culture (Experiment 1) is just what we might expect from the constitutions of the two groups. The wild culture probably contained many very diverse stocks; the conjugants probably were widely different in their gametic constitutions; so that there is the greatest possible opportunity for variation among their progeny. But all the members of the clone used in Experiment 2, by the theory of the pure line, have identical gametic constitutions. This may be and probably is highly heterozygous; but the diversity possible to the progeny of the different conjugants is limited by this heterozygosity. In Experiment 1 the diversity is limited only to the characters possible to 262 members of the species Paramecium caudatum, since every conjugant might possibly be different from every other; in Experiment 2 however this diversity is limited to the characters possessed by one individual Paramecium (the progenitor of the pure line used) and their possible recombinations. This fundamental difference in the constitutions of the two groups is very probably a cause of the production of greater diversity in form, and in the size, shape, and length of life of the individuals that never divided, mentioned on page 393.

The individuals used in the third experiment cannot be considered in this discussion, since they were derived from a small culture kept for some time in the laboratory, and the history of only 28 exconjugants is known.

Most of the abnormalities which have been described in the metazoa are explained as arrests in development; as suppressions of some part of the normal process of growth and differentiation. Some of my abnormalities answer to this description;

TABLE 4

Showing the frequencies of the different types of abnormals in the three experiments

TYPE	EXPERIMENT 1		EXPERIMENT 2		EXPERIMENT 3		TOTAL	
	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent
1	75	1.36	2	0.05	6	0.10	83	0.56
2	31	0.56			3	0.05	34	0.23
3	436	7.92	32	0.90	90	1.61	558	3.81
4	26	0.47			10	0.18	36	0.24
5	102	1.85	4	0.11	88	1.58	194	1.32
6	20	0.36					20	0.13
7	337	6.12	8	0.22	6	0.10	351	2.39
8	112	2.03			1	0.01	113	0.77
9	55	1.00	9	0.25	4	0.07	68	0.46
10			22	0.61	2	0.03	24	0.16
11	197	3.58	109	3.06	134	2.41	440	3.01
12	107	1.94	9	0.25			116	0.79
13	41	0.74	3	0.08	32	0.57	76	0.52
14	123	2.23	11	0.31	42	0.75	176	1.20
15	23	0.41	1	0.03	6	0.10	30	0.20
16	4	0.07	17	0.47	15	0.27	36	0.24
17	202	3.67	25	0.70			227	1.55
18	31	0.56	5	0.04			36	0.24
19	22	0.40	11	0.31	5	0.09	38	0.26
20	22	0.40	3	0.08	10	0.18	35	0.24
21	43	0.78					43	0.29
22	43	0.78	2	0.05	322	5.78	367	2.51
23	25	0.45	5	0.14			30	0.20
24	30	0.54					30	0.20
25	17	0.31					17	0.12
26	278	5.03	384	10.76	2891	51.94	3553	24.28
27	1028	18.69	919	25.76	682	12.25	2629	17.97
28	83	1.51	102	2.86	2	0.03	187	1.27
29	9	0.16			8	0.10	17	0.12
30	211	3.83	1688	47.32	373	6.70	2272	15.52
31	36	0.65	9	0.25			45	0.31
32	1	0.02	54	1.51	2	0.03	57	0.39
33	1430	26.00	87	2.44	54	0.91	1511	10.32
34	56	1.02	15	0.42	11	0.20	82	0.56
35	13	0.23			11	0.20	24	0.16
36	80	1.45	1	0.03			81	0.55
37	1	0.02	9	0.25			10	0.06
38	55	1.00					55	0.37
39	1	0.02	5	0.04	736	13.22	742	5.07
40	93	1.69	16	0.45	20	0.35	129	0.88
Total.....	5499	37.58	3567	24.38	5566	38.04	14632	100.00

certainly the individuals that never divided, the double and the monster forms, and those abnormal races in which the division rate is very much lowered, can be explained in that way. But in a few of the abnormal races the division rate was normal, and there was very little tendency to die out; indeed they showed no abnormal characters at all except the development of a slightly bizarre form. Race C is a good example of such a race. It lived for 191 days, had an average division rate of 1.16 per day, and was consistently abnormal throughout its history.

The mortality of the majority of the abnormal races was however considerably greater than that of the normal races. As the latter were all discontinued within a few days after conjugation, nine days being the usual length of time they were kept, no exact comparison can be made between their mortality and that of the abnormal races. However, they may be compared in a few ways, that show there are differences between them in vitality and tendency to die out. In each of the three experiments a large proportion of the abnormal races died within two weeks after conjugation, only a few races being kept for any length of time. In Experiment 1 there were 21 abnormal races; 14 per cent (3) of these lived for over a hundred days (105, 131, 191); 29 per cent were lost or discontinued after, on the average, 9 days of life; 12 (57 per cent) died after an average length of life of 15 days, and an average number of generations, 6. This gives an average division rate of 0.4 a day. The normals, discontinued 9 days after conjugation, had an average division rate of 1.12 a day. The facts in the other experiments are very similar to these; it is evident in all three that the abnormal races have, as a rule, a lower vitality and a greater degree of mortality. I explain this as largely due to the fact that the abnormal forms are hindered in their locomotion by their abnormal shape and so have not the normal facilities for meeting the exigencies of their existence. They often lie motionless on the bottom of the dish or slide for long periods; it was this lack of energetic movement which made possible camera lucida drawings of so large a proportion of them. It is probably for this reason that so few abnormals are found in the usual culture.

VI. THE ABNORMALITIES AS HEREDITARY CHARACTERS; VARIATION, INHERITANCE, AND SELECTION

As we have seen, the abnormalities which we are considering arise in consequence of conjugation. If half of a given stock are allowed to conjugate, the other half not, the former develops many of these abnormal races, while the latter develops none. This shows that the abnormalities cannot be considered due to infection, nor their reappearance in the stocks to the handing on of an infecting organism.

Since some lines are quite without abnormalities, while in others, under the same conditions, the abnormalities reappear for generations, it is clear that the tendency to abnormality is inherited. That is, the difference between a stock that thus produces abnormal individuals and one that does not, lies in the constitutions of the stocks themselves, and is something that is transmitted during vegetative reproduction.

Such hereditary diversities occur not only between normal and abnormal stocks, but also among the abnormal stocks themselves. Precise types of abnormality are indeed not inherited exactly from parent to progeny; within a given line as we have seen there is great variation as to whether abnormality appears at all in a given individual, and as to the precise kind that occurs when the individual is abnormal. Nevertheless, as before set forth, certain types of abnormality are particularly common in some lines, other types in other lines. The diverse lines differ hereditarily in respect to something of which the diverse typical abnormalities are the outward results. It is only by keeping in mind the characteristic differences between lines that we shall be able to grasp their relation to the problems of heredity.

The hereditary diversities thus far mentioned are between lines derived from diverse exconjugants. If anything like Mendelian inheritance occurs in infusoria, we could well expect such lines to show hereditary differences; this is of course as a rule true in any organism after the union of two parents to produce progeny.

On the other hand, in vegetative reproduction, and in general in long continued uniparental reproduction of any sort, a remark-

able constancy in hereditary characteristics has been generally reported. All the progeny thus coming from a single parent have seemed uniform in their hereditary characteristics, though they may differ in their bodily appearance. And this is quite in agreement with the known cytological processes accompanying the two types of reproduction. In biparental reproduction there is a reduction and recombination of the nuclear elements, of precisely the same sort as the variation and recombinations of characters in the progeny in Mendelian inheritance. In uniparental reproduction, particularly of the vegetative kind,[2] such nuclear reductions and recombinations are not known; and the uniformity of the progeny is in agreement with this.

These relations, with others not necessary to recount here, have given origin to the conception of the genotype as the hereditary constitution, in contradistinction to the bodily appearance. The genotype is commonly held not to change in vegetative reproduction, or but rarely, and then by marked sudden steps, or mutations. In biparental reproduction the genotype does indeed change, but seemingly by mere shiftings and recombinations, in numerically predictable ways; so that the relations here are quite in agreement with the condition sketched above for uniparental reproduction.

A somewhat rigid, stereotyped scheme of heredity naturally results from the view of the facts as just set forth; in particular, evolution by gradual change, guided by natural selection, appears to be excluded. This becomes still more marked if we conclude with Bateson ('14) that all mutations consist in the dropping out of factors. However, certain investigators in genetics oppose this rigid view, holding that, over and beyond Mendelian recombinations, hereditary variations of slight degree are frequently occurring, so that evolution may well be continuous and guided by selection. The recent papers of Castle give typical expression to this point of view.

[2] In their recent description of endomixis during the vegetative reproduction of P. aurelia, Woodruff and Erdmann observed neither reduction nor fusion of nuclear elements.

If hereditary variations are frequently occurring, aside from Mendelian recombinations, it should be possible to find them in vegetative reproduction. Here we are freed from the mixing of types which makes these relations so difficult to interpret in biparental reproduction. The hereditary abnormalities with which the present study deals seem to offer a favorable opportunity for the study of this matter. Within the same line of vegetative descent we find individuals that are in appearance normal, others that are outwardly abnormal. Can we by continued selection of normal individuals on the one hand, of abnormal individuals on the other, break our single stock into two or more, differing in hereditary constitution?

Experiments in selection

To answer the question just proposed, selection was carried on for many generations in a considerable number of abnormal stocks.

As before set forth, some of the races in which abnormalities occurred gradually changed character and became entirely normal. In other races both normals and abnormals appeared for long periods, giving opportunity for long continued selection. We will first take up the large race C, of Experiment 1.

Figures 10 and 11 give extracts from the pedigree of race C. This race, derived from exconjugant 101a, of Experiment 1, was kept for 191 days and produced during that time 4710 individuals in the observed cultures; 2683 of these were abnormals. The early history of this race is shown in chart 1.

CHART 1

Early history of Race C

(*n* = normal; *ab* = abnormal)

December 2	5	7	9	11	13	15	17
					8n —1	4n —1	Discontinued
1n—1	4n—4	8n—2	8n—1	4n—1	1ab—1	1ab—1	Dead
					1ab—1	1ab—1	Race C

In this and in the succeeding charts the first figure under each date shows the number of animals present in that line on that date; *n* means that these were normal; *ab* means that they were abnormal. The second figure, following the dash, denotes the number chosen to carry on the slide line, the others being put into

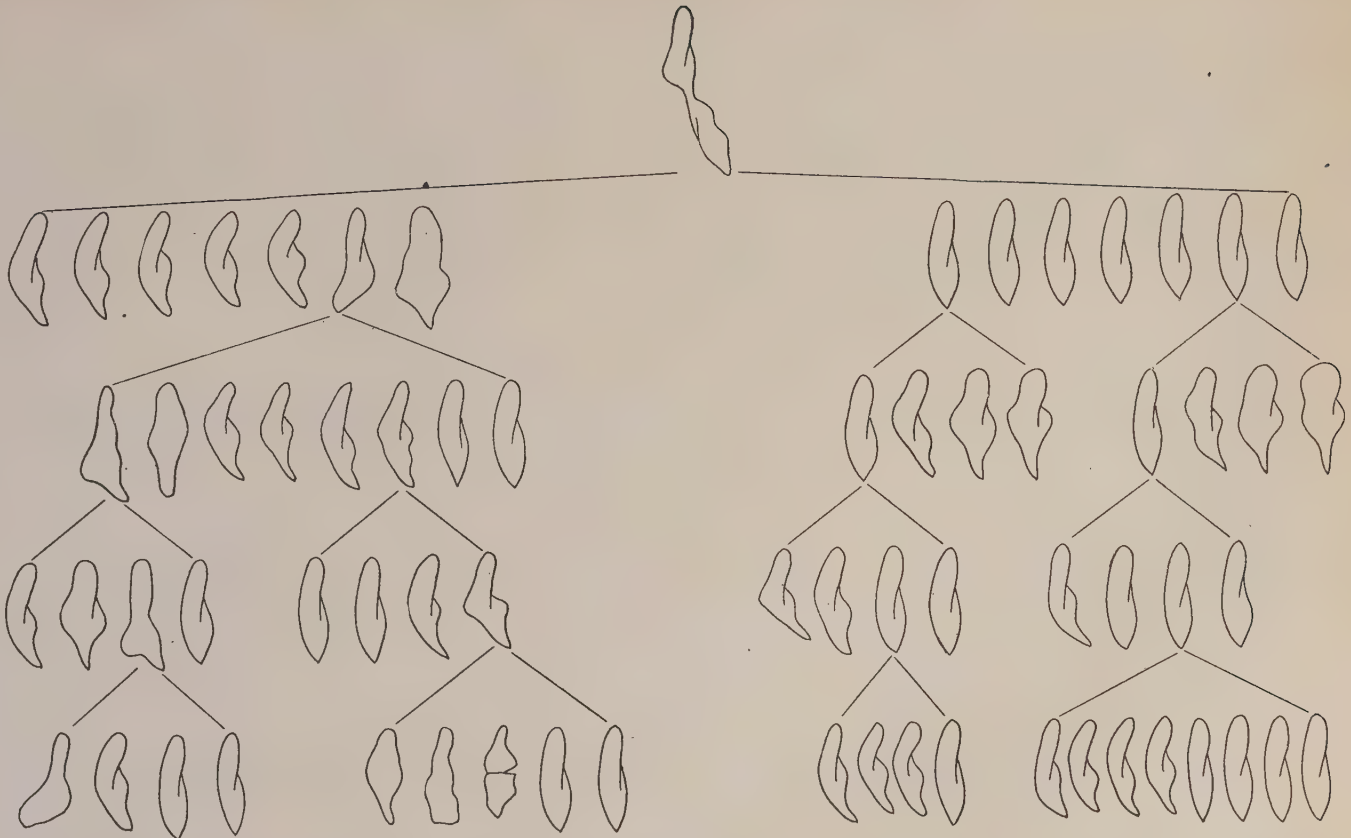


Fig. 10 Extract from the pedigree of Race C, showing on the left side a line in which abnormals were selected; on the right side a sister line in which normals were selected. The persistent appearance of the abnormalities in both lines, regardless of the selection, is evident. It will be noticed that a large proportion of the abnormals are of the type curved toward the oral side.

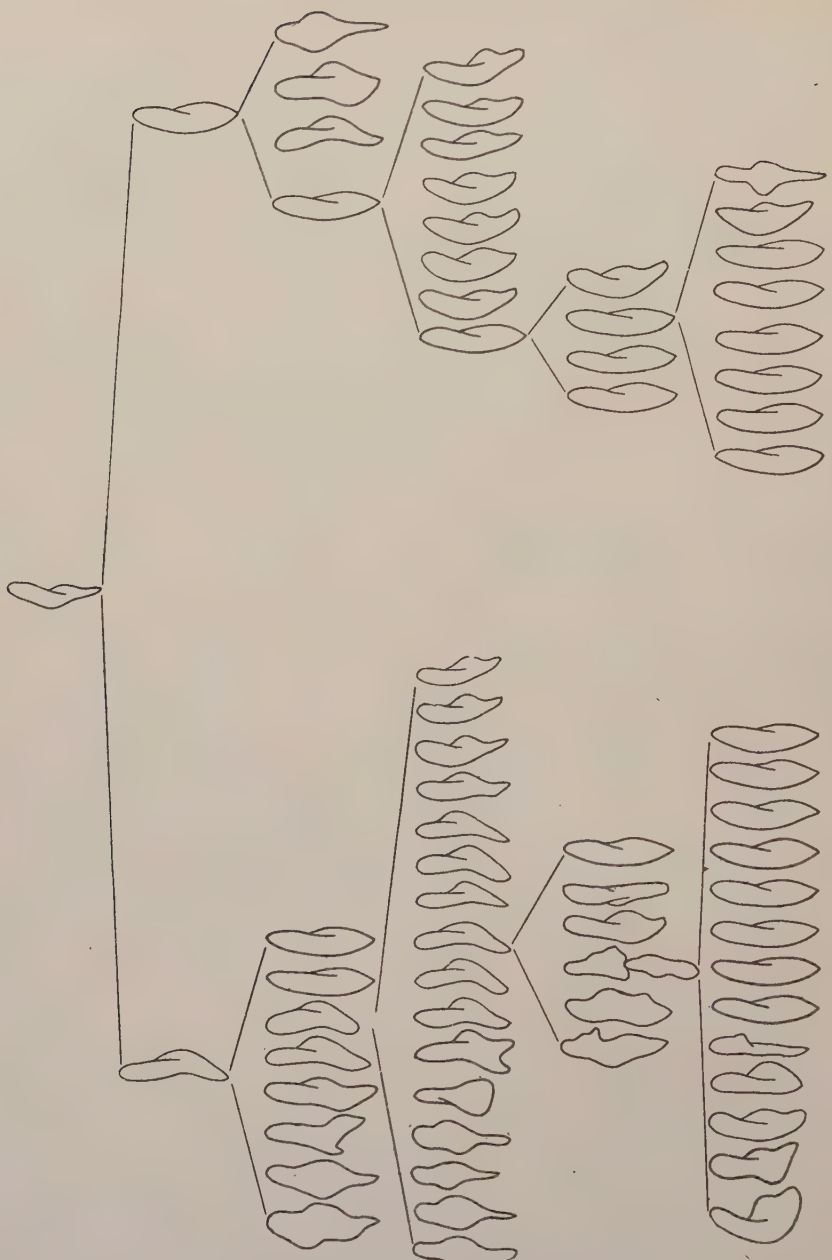


Fig. 11 Same as figure 10, but from a different group of lines.

bottle cultures, or discarded. In a number of the charts the second figure is omitted since the selection was the same on every date, one animal of a particular kind being always chosen. When both normals and abnormals are present in a single line (Chart 2) the kind which are entirely discarded are placed above, the kind from which one is chosen is placed below, each with its number. *D* means that on that date that line died out. Chart 1 therefore reads: On December 2 the normal exconjugant was isolated; December 5, it had divided to form four normals, all of which were kept; December 7, these had divided into eight normals, two of which were kept; these two had divided on December 9 to eight normals, one of which was kept; December 11, this one had given rise to four normals, one of which was kept; December 13, this one had given rise to two abnormals, both of which were kept, and to eight normals, one of which was kept; December 15, the normal had divided to form four, one of which was kept, and the two abnormals, neither of which had divided, were both kept; December 17, the normal line was discontinued entirely, one of the abnormal had died, and the other was kept and gave rise by repeated divisions to all the later individuals belonging to Race C.

Race C therefore appeared to be entirely normal for eleven days after conjugation, at the end of that time producing two abnormals, one of which was double, the other small and deformed. This small one gave rise to all the later 4681 observed individuals of this race, comprising 303 generations. In 34 lines of this race a continuous selection of normals was made, in one case for 32 days and 24 generations. The data from these lines is given in table 5. Their character was not changed in any way by this selection; the average proportion of abnormality for these 34 lines is only 2 per cent less than that of the race as a whole (table 3). In one line only normals were produced for as long as six days, the line at the end of that time again producing abnormals. The history of this line with a few of the others is given in chart 2. In every case one normal was selected each

TABLE 5

Data from the 34 normal-selected lines of Race C

GROUP	NUMBER OF LINES	NUMBER OF DAYS SELECTION CARRIED ON	NUMBER OF GENERATIONS OF NORMALS PRODUCED	NUMBER OF NORMALS	NUMBER OF ABNORMALS	PER CENT ABNORMAL
2	5	14	8	36	33	48
3	29	32	24	233	294	56
Total	34			269	327	55

day to carry on the line. It is evident that this selection has had no effect on the character of these lines.

CHART 2

History of six normal-selected lines of Race C
(n = normal; ab = abnormal; D = died out)

April 24	26	28	30	May 2	4	6	8	10	12	14	16	18	20	22
					6ab	1ab								
					10n	3n	D.							
				1ab	7ab									
				3n	6n	D.								
					9ab	2ab	5ab							
	3ab	1ab	4ab		7n	8n	2n	D.						
7n	1n	3n	4n		10ab									
					6n	D.								
				1ab	6ab									
				3n	2n	D.								
					20ab	2ab				2ab	3ab	3ab	2ab	2ab
					12n	4n	2n	1n	2n	2n	1n	1n	6n	2n

In 43 lines of race C a continuous selection of abnormals was made, in one line for 40 days and 37 generations. Their character was not changed by this sort of selection; their proportion of abnormality is the same as that for the race as a whole (table 3). The data from them is given in table 6, and the histories of a few in chart 3. In very case one abnormal was chosen on each day to carry on the line.

CHART 3

(n = Normal; ab = abnormal; D = died out)
History of five of the abnormal-selected lines of Race C

May 10	12	14	16	18	20	22	24	26	28	30
			2n	1n			2n	2n		
			2ab	3ab	4ab	2ab	2ab	2ab	D.	
			4ab	2ab	4ab	4ab	1ab	1ab	D.	
					4n		4n	2n		
			2ab	3ab	4ab	3ab	4ab	2ab	2ab	D.
				3n	1n	2n				
			2ab	3ab	3ab	2ab	8ab	4ab	D.	
					3n	1n	3n			
6ab		1ab	3ab	2ab	4ab	2ab	3ab	1ab	2ab	D.

Three times in the history of this same race all of the individuals died with one exception; in every case this single sur-

viving individual was an abnormal animal which gave rise by repeated divisions to the further representatives of its race. On two of these occasions the two groups of lines which rose from the two first daughter cells of this single abnormal animal were treated differently; in one group the most normal individuals were selected; in the other group, sister to the first, the most abnormal were selected. The data for these two pairs of groups is given in table 7. In this table, one abnormal-selected line in the first set lived longer than 56 days; in the second set one normal-selected line lived longer than 20 days; both however for purposes of comparison are counted in this table as having died out at the same time with the other lines of their sets.

TABLE 6

Data from the 43 abnormal-selected lines of Race C

GROUP	NUMBER OF LINES	NUMBER OF DAYS SELECTION CARRIED ON	NUMBER OF GENERATIONS OF NORMALS PRODUCED	NUMBER OF NORMALS	NUMBER OF ABNORMALS	PER CENT ABNORMAL
1	3	40	30	58	83	59
2	9	36	19	103	126	55
3	25	32	31	135	163	55
4	6	18	13	49	93	65
Total	43			345	465	57

TABLE 7

Data from two sets of sister groups of lines; in one group of each set the most abnormal were selected; in the other group, the most normal

SET	GROUP	NUMBER OF LINES	NUMBER OF DAYS SELECTED	NUMBER OF GENERATIONS	NUMBER OF NORMALS	NUMBER OF ABNORMALS	PER CENT ABNORMAL
1	Abnormal-selected	15	56	48	387	489	56
	Normal-selected	15	56	50	486	834	63
2	Abnormal-selected	20	20	25	131	157	54
	Normal-selected	20	20	24	211	320	60

With these two exceptions, one abnormal-selected and the other normal-selected, the two groups in both sets are very much alike. They show a great deal of similarity in length of life, number of generations, and proportion of abnormality, the diverse selection having had no effect on the character of the lines. Indeed, in both sets, the lines of the normal-selected group show a larger proportion of abnormals.

Thus in line C we have a race in which long continued selection has no effect on the inheritance of abnormalities. And these results are typical of a large number of races—all those classified on page 399 as class 2 (97 races all together). In all of these races where such a procedure was possible the selection of normals was carried on as long as the race lived, in an attempt to establish a normal line; but with all these races this effort failed. The normals selected continued indefinitely to produce abnormal progeny in the original proportions. With these races therefore the results of continued selection are the same as those obtained by the majority of investigators in uniparental reproduction: selection does not alter the inherited constitution of the line nor produce two genotypes from one.

In another set of abnormal lines however, different results were reached. In twenty-five races of our three experiments the single race was split up by selection into hereditarily diverse groups, one group composed of lines that continued to produce abnormals, the other composed entirely of normals. The main facts as to these twenty-five races are given in table 8. Many of these lines were kept but a short time, so there might be doubt as to the precise significance of the results from them. Certain lines however were kept for a very large number of generations and give conclusive results. This was the case with the lines *A* and *B* of Experiment 1, and with the six lines of Experiment 3. Some details will therefore be given as to these races.

The history of race A may be taken as a type. The exconjugant from which this arose gave rise to normal individuals only for seven days, or until December 9, when eight abnormals and ten normals were found on the slide. After this the race did

TABLE 8 (first part)

Data from the 25 races of the three experiments which were affected by selection

EXPERIMENT	RACE	ABNORMAL LINES					
		Number	Days	Generations	Normals	Abnormals	Per cent abnormal
1	48a	3	27	9	27	6	18
	53b	1	11	3	2	2	50
	93b	4	23	10	38	9	19
	105b	1	17	2	1	1	50
	A	178	131	74	524	850	63
	B	314	105	83	1328	1788	57
2	2a	1	15	4	2	7	78
	4a	2	23	5	6	7	54
	4b	4	27	14	52	22	30
	7a	2	27	15	34	19	36
	10a	1	13	4	8	3	27
	10b	24	27	26	293	323	52
	18a	20	27	28	634	748	54
	40b	1	17	6	6	2	25
	41a	1	11	4	6	9	60
	62a	1	11	5	5	3	38
	69a	9	27	25	172	213	55
	83b	7	27	15	40	22	35
	87a	7	27	15	55	23	29
3	54b	4	54	33	673	117	15
	55b	7	54	53	1785	467	21
	56a	18	77	62	3650	1121	23
	56b	20	77	65	2818	567	17
	59a	30	77	32	1051	369	26
	59b	73	77	50	3201	1643	34
Total...		733			16411	8341	
Average		29	40	26	656	334	39

not return to complete normality, but always showed a large proportion of abnormal forms among its members. For some time all the normal individuals were discarded and all the abnormals kept. By December 23 this procedure had resulted in so many lines (178) that all but 45 of the most abnormal were discarded. These 45 very abnormal lines were grouped for convenience into 13 categories. The genetic history of the lines

TABLE 8 (second part)

Data from the 25 races of the three experiments which were affected by selection

EXPERIMENT	RACE	X*	NORMAL LINES					
			Number	Days	Generations	Normals	Abnormals	Per cent
1	48a	7	1	6	7	20		
	53b	7	1	5	7	7		
	93b	9	4	6	5	50		
	105b	1	1	5	2	4		
	A	62	6	26	22	134		
	B	5 to 49	3	20	21	126		
2	2a		1	4	8	31		
	4a		1	6	3	6		
	4b	2	1	6	4	77		
	7a	8	1	4	3	7		
	10a	8	1	4	3	10		
	10b	4	1	4	3	8		
	18a	18	4	6	9	75		
	40b		1	8	3	8		
	41a	4	1	8	3	8		
	62a	6	1	6	4	16		
	69a	8	2	4	6	50		
	83b		1	12	4	6		
	87a	8	4	12	6	53		
3	54b	9 to 42	15	35	20	3589		
	55b	9 to 11	2	12	13	272		
	56a	9 to 50	8	37	24	936		
	56b	9 to 44	11	24	26	1164		
	59a	9 to 37	2	47	35	425	3	0.5
	59b	37 to 53	12	39	27	1334		
Total...			86			8346	3	
Ave.....		24	3	14	11	334	0.12	0.2

* X is the number of days that the selection of normals went on before the normal lines were isolated.

which made up these groups is given in chart 4. Two of these groups of lines, A2 and A6 died very soon; the other lines lived for some time and the data from them is given in table 9.

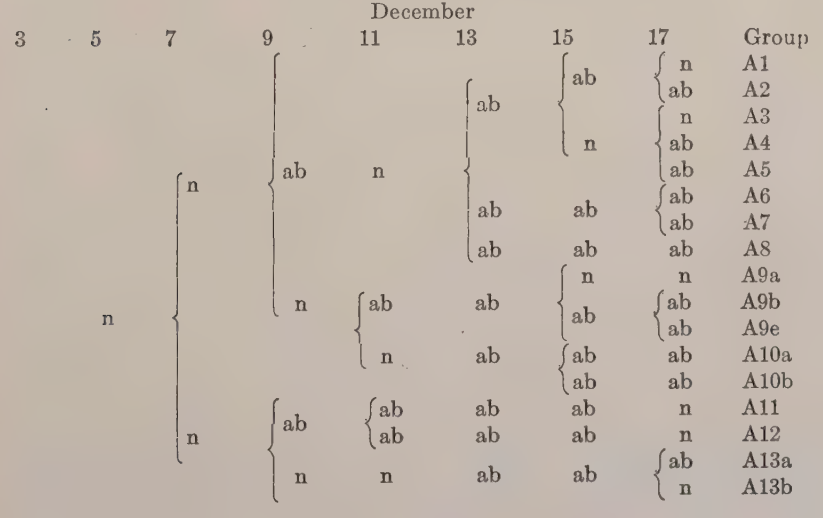
TABLE 9

Data from eleven groups of Race A

GROUP	LENGTH OF LIFE IN DAYS	NUMBER OF GENERATIONS	NUMBER OF NORMALS	NUMBER OF ABNORMALS	PER CENT ABNORMAL
A1	31	16	22	35	61
A3	69	40	34	85	71
A4	37	22	13	44	77
A5	131	64	61	182	75
A7	33	16	18	54	75
A8	47	16	14	55	80
A9	69	30	35	154	81
A10	25	11	31	19	48
A11	27	11	13	26	67
A12	51	13	26	54	67
A13	115	74	391	132	25
Largest	131	74	391	182	81
Total			658	850	56
Average	58	28	60	77	56

CHART 4

Genetic history of the thirteen groups of Race A
(*n* = normal; *ab* = abnormal)



After December 23 every one of the lines belonging to race A was carried on in two parts or sub-lines; in one sub-line the most normal individuals were selected; in the other sub-line the most abnormal individuals were selected. This procedure kept going a number of normal-selected lines up to as many as 40; and an equal number of abnormal-selected lines. In almost all of the normal-selected lines the continuous selection of normals was not possible; some generations were entirely abnormal, no normals at all being produced. But 62 days after this normal selection had begun, one normal was isolated which gave rise to six lines in which the continuous selection of normals was possible for some time before they died out. Their history is given in chart 5, and the data afforded by them in table 10. The largest of these six lines was kept for 26 days after the continuous selection of normals was begun and gave rise to 22 generations of normals. There were 42 individuals in the observed cultures of this one line; one of these was abnormal; all the rest were normal.

TABLE 10

Data from the six lines of Race A in which the selection of normals was continuous

SELECTION CONTINUOUS					LINES ENTIRELY NORMAL		
Days	Generations	Normals	Abnormals	Per cent abnormal	Days	Generations	Individuals
12	10	21	0	0	12	10	21
10	10	12	0	0	10	10	12
6	6	8	0	0	6	6	8
22	18	32	1	3	10	7	11
14	13	20	0	0	14	13	20
26	22	41	1	2	20	15	25
Greatest 26	22	41	1	3	20	15	25
Total		134	2	1			97

As all the animals of these six lines were descendants of one normal individual present on February 27 (chart 5), they can all be counted together as one group, which will give 134 normal

individuals to 1 abnormal individuals in 21 generations. This is a very low proportion indeed as compared with that for the race as a whole (56 per cent). Moreover, every one of these six races was entirely normal for some time before it died, as

CHART 5

Genetic history of six lines of Race A in which the selection of normals was continuous

(*n* = normal; D = died out)

Line	Feb. 27	Mch. 1	3	5	7	9	11	13	15	17	19	21	23	25	27
A13b1	1n	4n	4n	3n	4n	2n	4n	D.							
				4n	4n	4n	D.								
			4n	4n	D.										
								1ab							
			3n	2n	2n	2n	4n	5n	4n	2n	4n	4n	D.		
				4n	4n	2n	2n	8n	D.						
				7n	1n	4n	4n	4n	8n	4n	4n	2n	2n	1n	D.

shown in the table. Figure 12 gives that part of the pedigree of race A which includes these six lines.

In 24 of the abnormal selected lines abnormals were produced in every generation for some time and their selection was therefore continuous. The history of six of these lines is given in chart 6. Table 11 gives the data from all of them. The largest line was kept for 36 days after the selection of abnormals became

CHART 6

Genetic history of six of the lines of Race A in which the continuous selection of abnormals was made

(*n* = normal; *ab* = abnormal; *D* = died out)

December 21	23	25	27	29	31	January 2	4	6	8	10	12	14	16	18
2n		1n												
2ab	2ab	2ab	1ab	3ab	1ab	1ab	1ab	1ab	D.					
1n														
1ab	2ab	1ab	1ab	D.										
1n														
1ab	1ab	1ab	1ab	D.										
2n														
2ab	3ab	1ab	D.											
1ab	1ab	4ab	1ab	2ab	2ab	2ab	2ab	1ab	2ab	4ab	2ab	2ab	1ab	D.
	1n	1n												
1ab	1ab	1ab	1ab	1ab	1ab	1ab	1ab	1ab	D.					

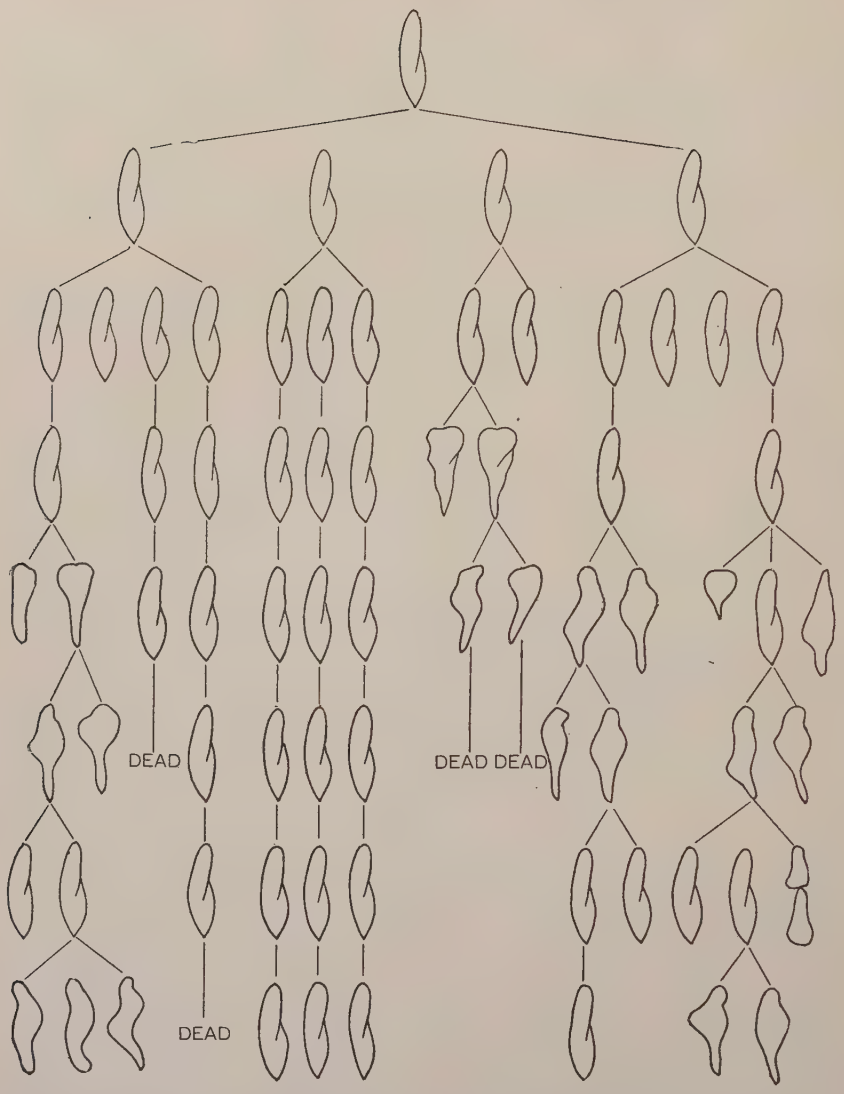


Fig. 12 Extract from the pedigree of Race A which includes the origin of the six normal lines produced by this race. In the abnormal lines only a few of the animals in each generation are shown; in the normal lines, only one in each generation.

continuous, and gave rise to 16 generations. Two normals and 18 abnormals appeared in the observed cultures of this line. The proportion of abnormality (79 per cent) shown by all these lines taken together is much higher than that shown by the race as a whole (56 per cent). Figures 13 and 14 give part of the pedigrees of three of these lines.

TABLE 11

Data from the 24 lines of Race A in which the selection of abnormals was continuous

SELECTION CONTINUOUS					LINES ENTIRELY ABNORMAL		
Days	Generations	Normals	Abnormals	Per cent abnormal	Days	Generations	Individuals
16	9	4	13	76	10	6	10
18	6	3	6	67	12	3	3
8	2	1	2	67	6	2	2
6	1	0	1	100	6	1	1
8	1	1	1	50	6	1	1
6	4	2	4	67	4	2	3
6	2	0	2	100	8	1	2
18	6	8	8	50	10	1	1
36	16	2	18	90	28	12	14
20	3	3	3	50	12	1	1
16	5	5	6	55	8	2	2
22	11	4	11	73	8	3	3
24	8	6	8	57	12	2	2
20	9	4	8	67	8	2	2
22	8	3	6	67	12	2	2
20	6	0	6	100	20	6	6
24	5	0	5	100	24	5	5
8	4	1	4	80	6	3	3
12	4	1	4	80	10	3	3
14	4	2	4	67	10	2	2
12	3	0	3	100	12	3	3
10	2	0	2	100	10	2	2
6	8	8	10	56	2	1	1
14	8	22	12	35	10	5	5
Greatest 36	16	22	18	100	28	12	14
Total.....		80	147	65			79

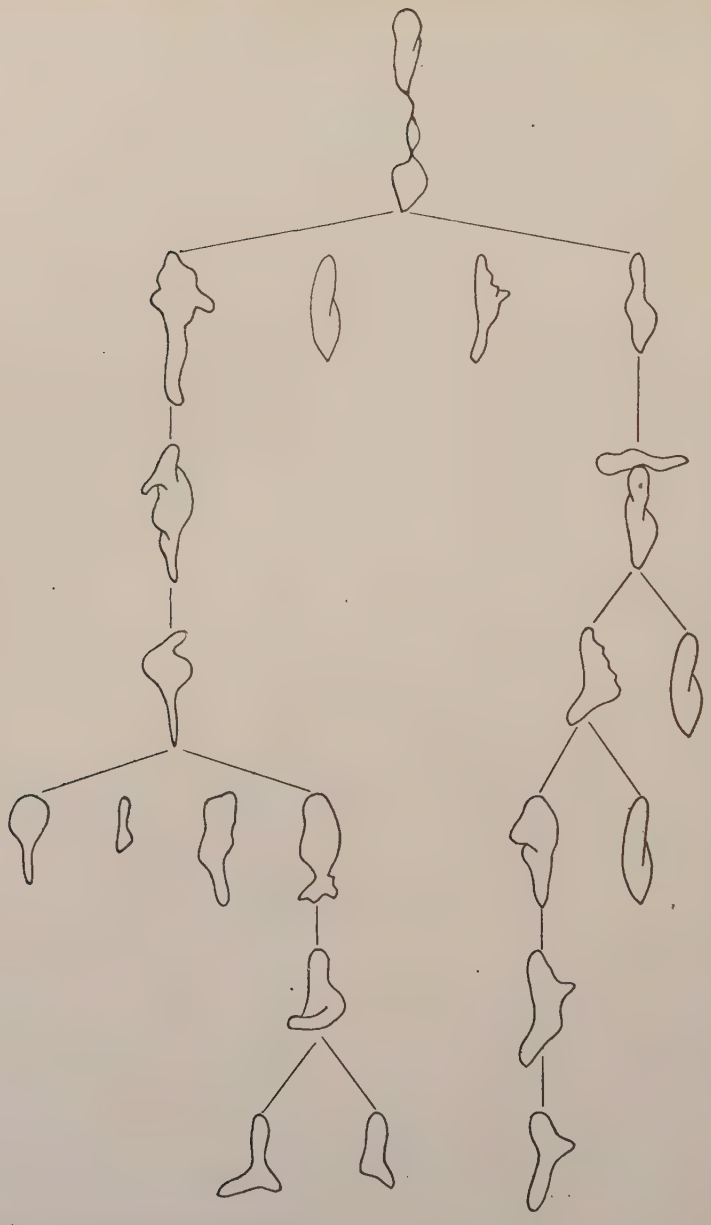


Fig. 13 Part of the pedigrees of two of the abnormal-selected lines of Race A.

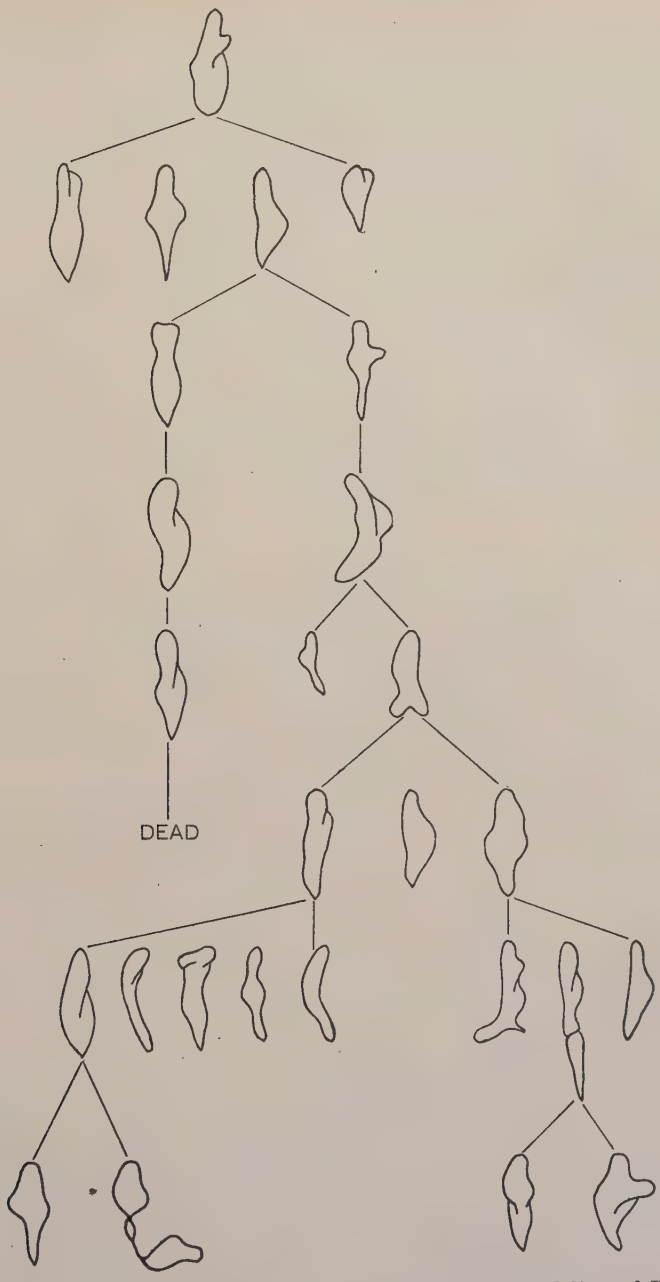


Fig. 14 Part of the pedigree of another abnormal-selected line of Race A.

We have therefore in race A a group of individuals all descended by vegetative reproduction from one animal, exconjugant 1b, which for 74 generations and 131 days constantly produced abnormals in an average proportion of 56 per cent of all the individuals of the race. From this clone, having this heritable character, abnormality, were obtained through the action of selection, two diverse groups of individuals. One group had a constant proportion of abnormality, on the average, of 70 per cent; the other with almost total normality, the abnormality having been reduced to an average of 1 per cent; all of the lines were entirely normal for some time before they died out. In this clone therefore we have an inheritance of a variation, abnormality; and also we have permanent changes in this heritable variation, brought about by the action of selection.

TABLE 12

Data from fourteen groups of Race B

GROUP	LENGTH OF LIFE IN DAYS	NUMBER OF GENERATIONS	NUMBER OF NORMALS	NUMBER OF ABNORMALS	PER CENT ABNORMALS
B1	81	47	43	73	63
B2	81	67	107	80	43
B3	81	73	178	144	45
B4	105	83	292	338	54
B5	75	61	60	94	61
B6	61	46	46	67	59
B7	71	66	114	177	61
B8	73	58	66	118	64
B9	89	64	73	110	60
B10	103	74	145	143	50
B11	67	46	40	137	77
B13	65	41	38	66	63
B14	69	53	87	145	62
B15	71	15	52	96	65
Greatest	105	83	292	338	77
Total			1371	1788	56

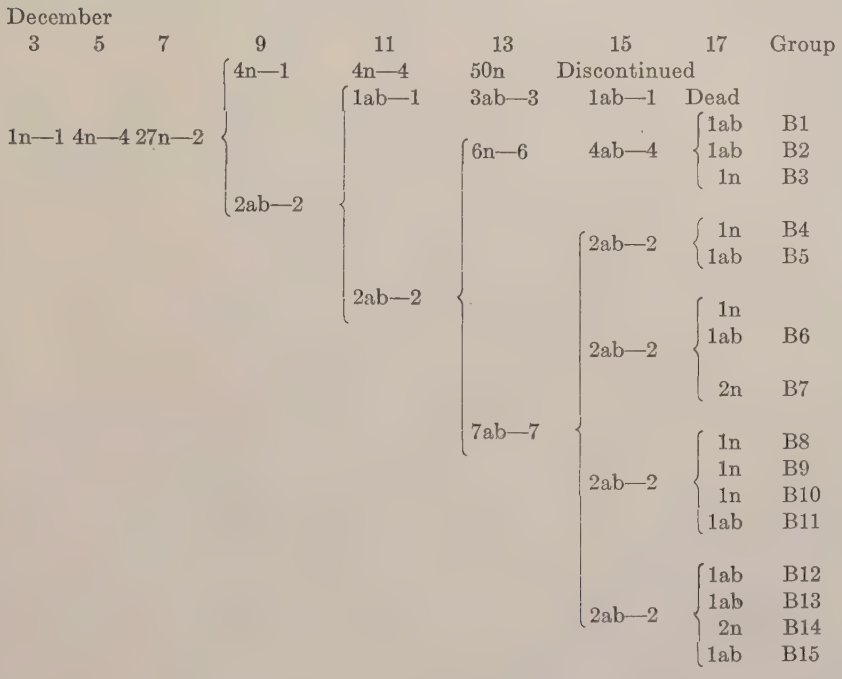
The history of race B shows some slight variations from that of race A. Its early history is shown in chart 7. It was en-

tirely normal until December 7, five days after conjugation. On that date two of the existing 27 normal individuals were chosen to carry on the race; one of these continued to produce only normals until it was discontinued six days later. By that time it had given rise to 53 normal individuals. This was the largest group of normals produced by race B.

CHART 7

(n = normal; ab = abnormal)

Early history of Race B and formation of the fifteen groups



The other normal kept on December 7 gave rise to all later individuals of race B, which were kept for 105 days, and 83 generations, and had an average proportion of abnormality of 56 per cent. The history of this race from this point on is exactly like that of race A. On December 23, 83 of the most abnormal lines were selected from the existing 314, and grouped (table 12).

Each one of the 83 lines was divided into two sub-lines, in one of which the most normal were selected, in the other the most abnormal. In six lines the continuous selection of normals was possible. Their history is given in chart 8, and table 13 gives the data from them. Two of these lines produced abnormals the last day they were kept, and a third was entirely normal for only four days before death; the selection has slightly decreased the proportion of abnormals produced, but has not eliminated the abnormal character. But the three other lines became entirely normal some time before death, as the table shows. Selection here has had a decided effect; has entirely eliminated the abnormal character.

CHART 8

Genetic history of the six lines of Race B in which the selection of normals was continuous

(n = normal; ab = abnormal; D = died out)

Line	January						February					
	20	22	24	26	28	30	1	3	5	7	9	
			1ab	4ab	2ab							
B2	4n	8n	2n	4n	2n	4n	8n	2n	4n	4n	D.	
B3		8n	4n	8n	6n	8n	8n	2n	4n	3n	D.	

Line	December								January								
	25	27	29	31	2	4	6	8	10	12	14	16	18	20	22	24	
			3ab	1ab	2ab												
B4b2		2n	1n	1n	1n	2n	1n	8n	2n	5n	2n	2n	4n	4n	8n	D.	
				2ab			1ab	3ab		3ab	1ab	2ab					
B4i1		2n	2n	2n	2n	2n	2n	1n	3n	1n	1n	2n	2n	4n	D.		
	3ab		2ab	2ab	1ab	2ab	1ab	2ab	1ab	1ab	3ab	1ab			1ab		
B7	1n	2n	2n	2n	2n	2n	1n	1n	1n	2n	1n	1n	3n	2n	7n	D.	
			2ab			1ab											
B15	2n	2n	2n	2n	1n	1n	D.										

In nine lines the continuous selection of abnormals was possible. The history of three of them is given in chart 9 and table 14 gives the data from them. The proportion of abnormality in most of these lines has been somewhat raised by this selection over that of the race as a whole; but not to such an extent as in

race A. Pedigrees of two of these lines are given in figures 15 and 16.

TABLE 13

Data from the six lines of Race B in which the selection of normals was continuous

SELECTION CONTINUOUS					LINES ENTIRELY NORMAL		
Days	Generations	Normals	Abnormals	Per cent abnormal	Days	Generations	Individuals
20	20	33	7	17	10	11	18
18	22	43	0	00	18	22	43
28	21	30	6	17	20	17	29
26	13	15	12	44	4	4	5
30	13	16	20	56	0	0	0
12	4	5	3	38	0	0	0
Greatest 30	22	43	20	56	20	22	43
Total.....		142	48	25			95

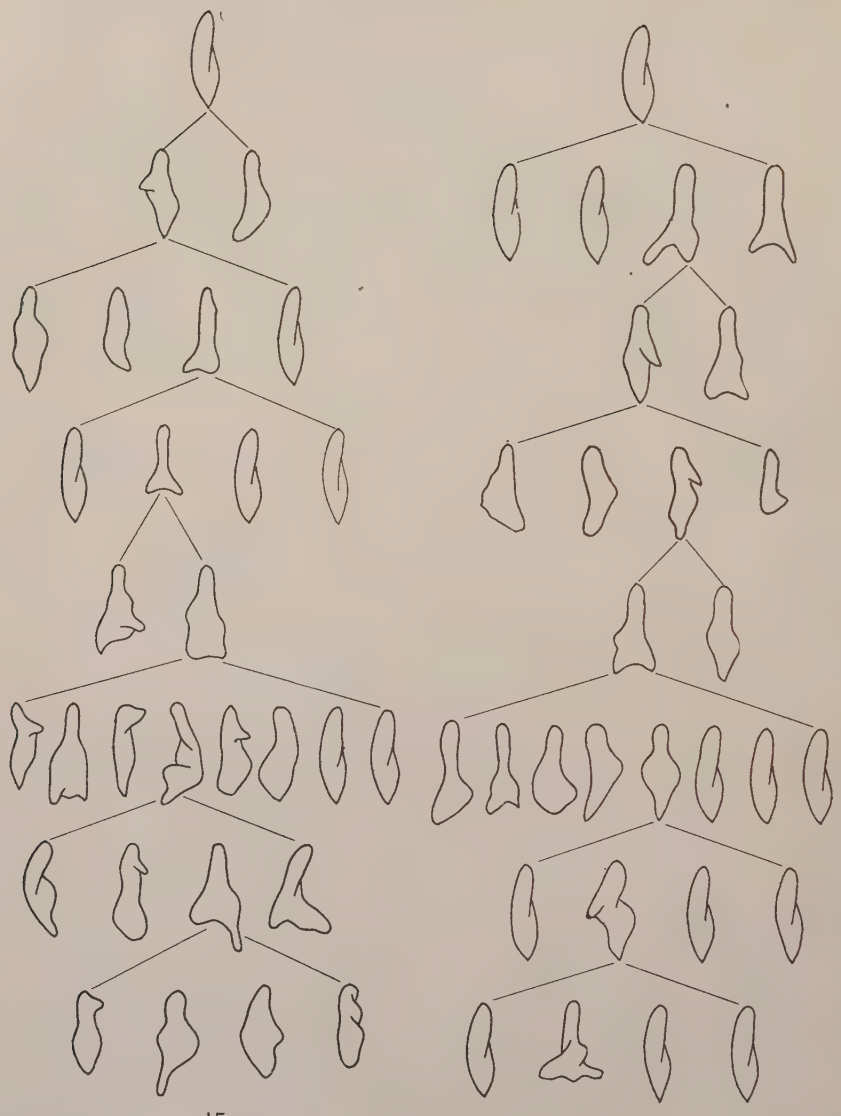
CHART 9

Genetic history of three of the lines of Race B in which continuous selection of abnormals was made

(*n* = normal; *ab* = abnormal)

Dec.					January								
31	2	4	6	8	10	12	14	16	18	20	22	24	26
1n		1n	1n	1n									
1ab	3ab	3ab	3ab	3ab	2ab	1ab	1ab	1ab	Dead				
2n				3n	3n	3n		2n		1n			
2ab	2ab	4ab	2ab	5ab	1ab	1ab	2ab	2ab	4ab	1ab	1ab	Dead	
	1n	3n		2n									
2ab	3ab	1ab	2ab	6ab	4ab	4ab	1ab	2ab	4ab	1ab	Dead		

We have therefore in race B a group of individuals constituting a clone, which after the fifth generation and the production of 32 individuals, gave rise to two diverse groups, with different hereditary characteristics. One group was entirely normal; the other group showed a large and constant proportion of abnormals. Later from this abnormal group, by continued selection in opposite directions, lines were isolated which showed



15 16

Fig. 15 Part of the pedigree of an abnormal-selected line of Race B.
Fig. 16 Part of the pedigree of another abnormal-selected line of Race B.

TABLE 14

Data from the nine lines of Race B in which the selection of abnormals was continuous

SELECTION CONTINUOUS					LINES ENTIRELY ABNORMAL		
Days	Generations	Normals	Abnormals	Per cent abnormal	Days	Generations	Individuals
20	9	2	20	83	8	5	5
18	8	4	11	73	10	2	2
18	6	5	8	62	8	2	2
24	11	14	16	53	2	1	1
18	9	1	10	91	14	8	8
22	13	6	20	77	12	8	11
22	10	13	15	54	2	2	3
24	13	11	15	58	2	1	1
14	5	2	6	75	12	5	5

hereditary differences in degree of abnormality. One set of lines showed a very low degree, three lines becoming entirely normal. The other set showed a very high degree of abnormality, one line having 90 per cent of abnormals.

We have then in race B the inheritance of a variation within the clone; and a splitting up of the clone, both with and without selection, into hereditarily diverse groups.

The six races of Experiment 3 underwent a most strict selection of normals throughout their history; and in every case this eventually brought about a change in the inheritance of the abnormality. In each race all of the individuals arising from the exconjugant were kept for the first six days; thereafter the abnormals were discarded and only normals kept, as far as possible. Abnormals were kept only when no normals were present with which to carry on the race. In all these six races this procedure had much the same effect. Some of their lines were not changed at all; they continued to produce abnormals from the normal cells selected. But other lines became entirely normal. In every case there was inheritance of the variations which had arisen within the clone. Figures 17, 18, 19, and 20 give pedigrees of four of these races, 56a and b, and 59a and b. All six races are very similar in their history. On January 17 none of the six had completed their first division; all had formed

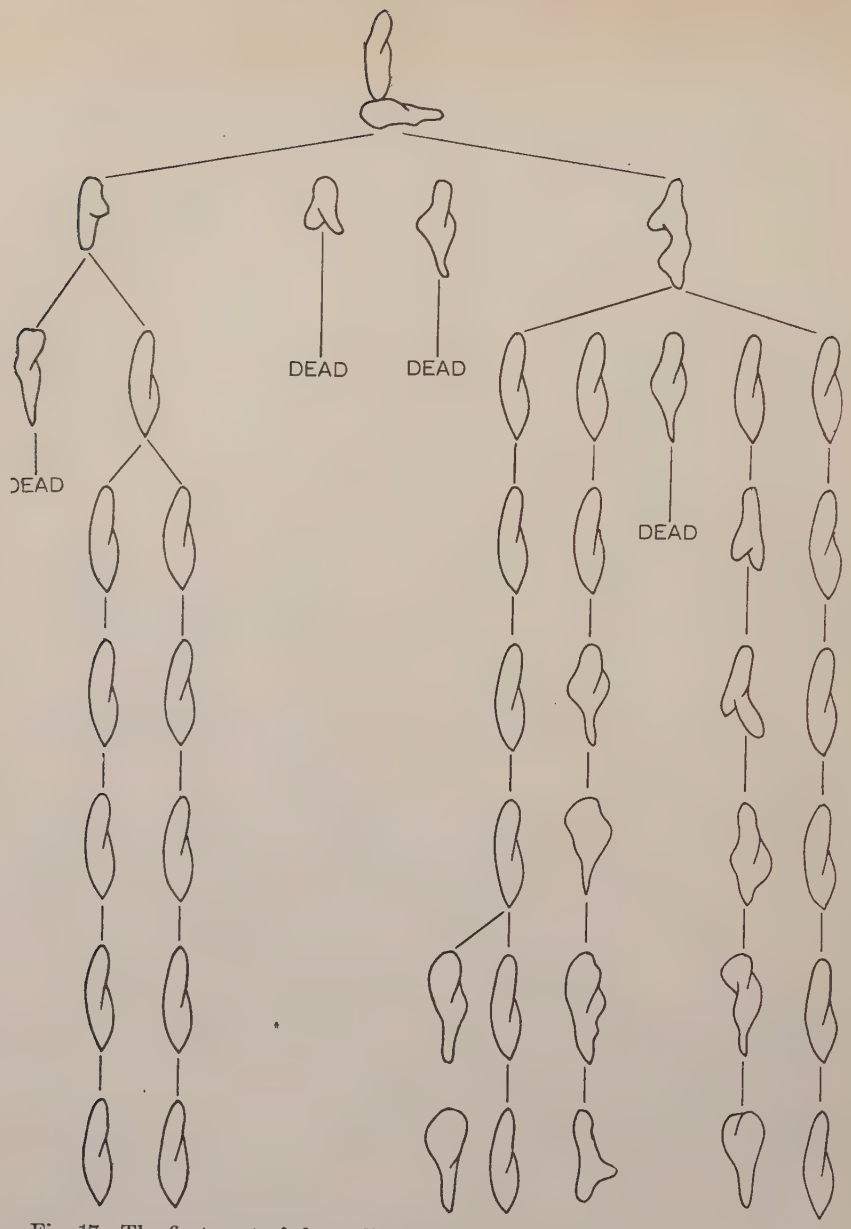


Fig. 17 The first part of the pedigree of *56a*, showing the origin of four of the normal lines. The other four normal lines were derived much later from one of the abnormal lines shown here. In this figure and in the succeeding ones, in each generation only those animals are shown which were selected to carry on the lines.

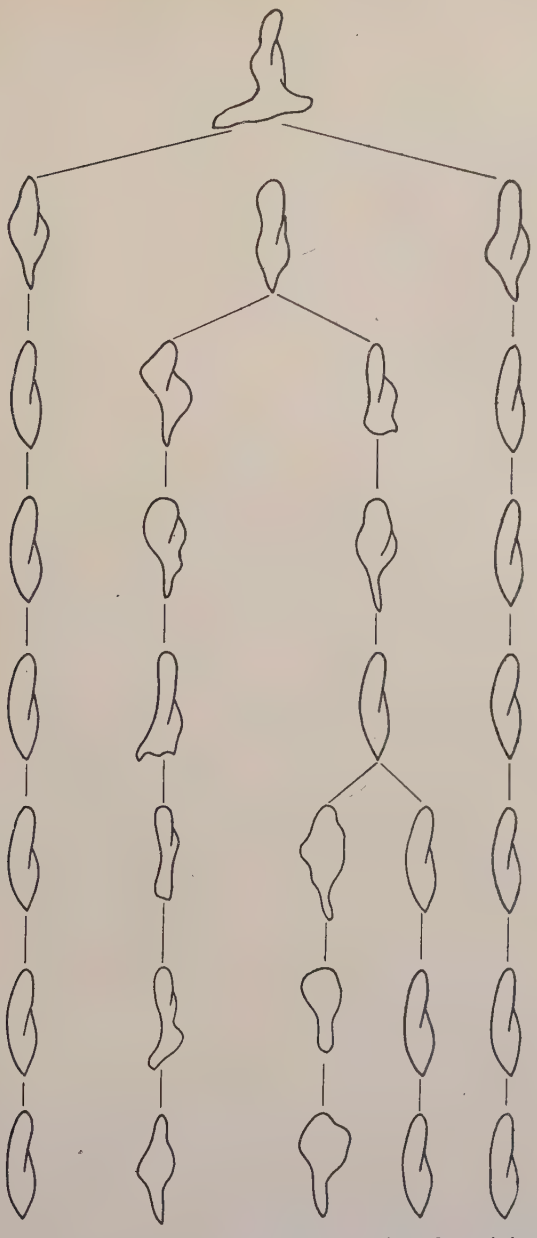


Fig. 18 First part of the pedigree of *56b*, showing the origin of three of the normal lines. The other eight normal lines were derived much later from the abnormal lines shown here.

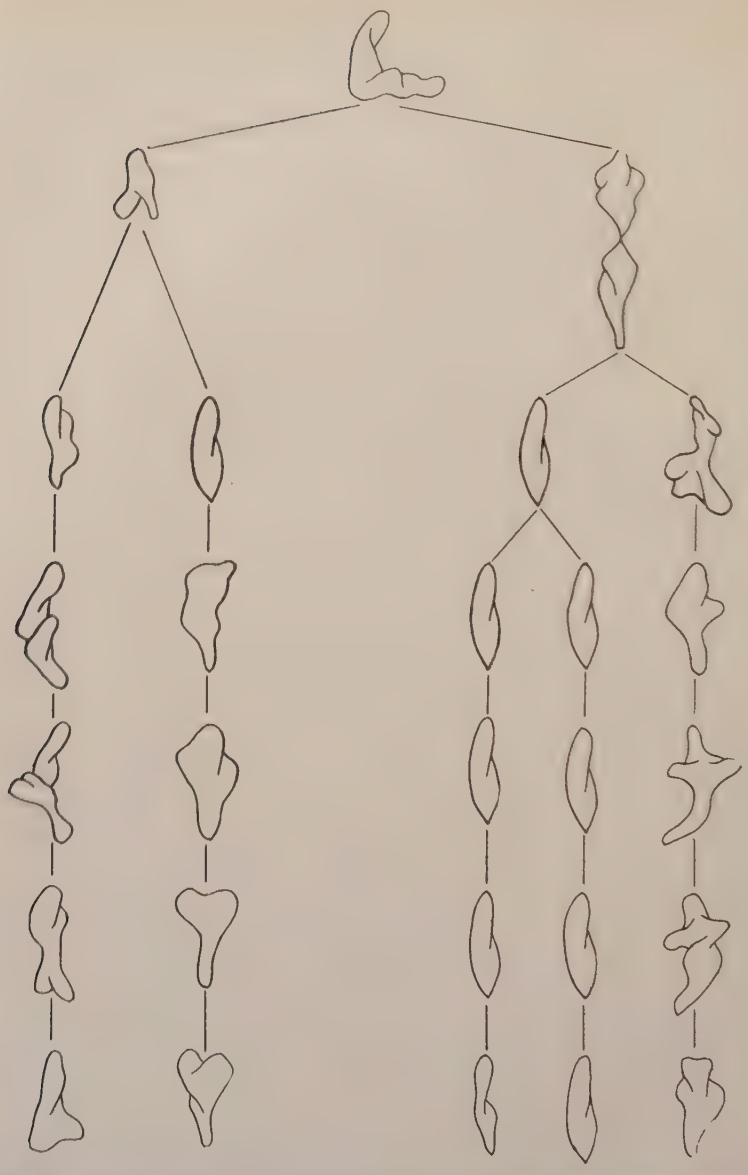


Fig. 19 The first part of the pedigree of *59a*, showing the origin of one of the normal lines. The other normal line was derived 32 days later from one of the abnormal lines shown here.

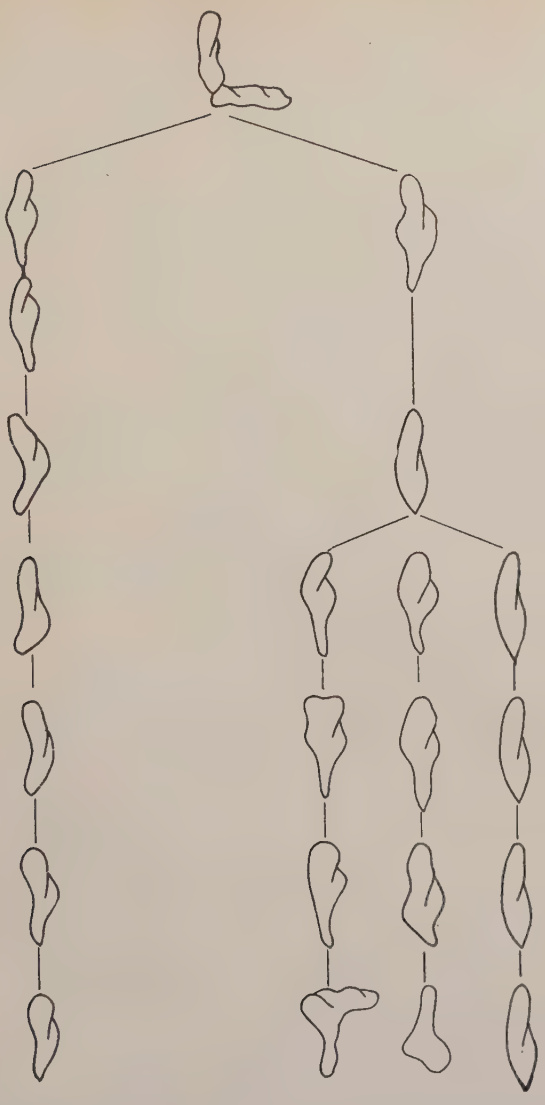


Fig. 20 The first part of the pedigree of *59b*, showing the origin of one of the normal lines. The other eleven normal lines were derived much later from the abnormal lines shown in this figure.

double monsters of the L variety. On January 19, exconjugant 56a (fig. 17) had divided to form four abnormals; two of these died without dividing further. One of the other two produced

one abnormal which died before dividing, and one normal which gave rise to two entirely normal lines which were kept for ten days and eleven generations. They comprised 115 observed individuals, all normal. The other abnormal present on January 19 divided to form one abnormal (which died before further division) and eleven normals. Nine of these were kept. Six of them gave rise to lines which remained entirely normal; three produced abnormal lines. Two of these abnormal lines remained abnormal throughout their history, never responding positively to the normal selection they underwent. From the other abnormal line five entirely normal lines were split off, kept for a number of generations varying from 6 to 24. Three of these normal lines were kept until April 1; their eight abnormal sister lines were also kept until April 1, 77 days after conjugation.

Since all six lines had very similar histories they will not be given in detail. The main facts as to the production of the normal lines can be gathered from the pedigrees (pages 436 to 439) and the table (pages 421–422).

Thus on the whole the work on selection shows that with relation to these abnormal characteristics heritable variations are in many races occurring during vegetative reproduction. By selection the effect of these variations may be accumulated, so that while one part of the race remains abnormal, or even increases the proportion of abnormal individuals, another part greatly decreases the proportion of abnormality, or becomes entirely normal. The general bearing of these results will be discussed after the rest of the facts have been brought out.

Relation to biparental inheritance

Does conjugation tend to produce similarity in respect to abnormality or normality between the progeny of the two individuals that conjugate? That is, if the descendants of one of the two members of a given pair are abnormal, is there a tendency for the descendants of the other member to be abnormal also? If a given stock is abnormal, is the stock derived from the *mate* of its progenitor likely to be abnormal also? Jennings and Lashley ('13, '13a) have shown that there is such a tend-

ency to resemblance between the stocks derived from the two members of a pair, in respect to fission-rate, death-rate, and size.

The question with relation to abnormalities may be attacked by the same methods employed by Jennings and Lashley. The problem presents itself as follows. From a certain number m of exconjugants (forming m/2 pairs) a certain number n of abnormal races are produced. In some cases both races derived from a pair are abnormal; in other cases only one; in others, neither. Is the number of cases where both races are abnormal greater than would be expected if the pairing had no relation to the distribution of the abnormalities? If so, this is evidence that the pairing tends to make the two races alike in this respect.

Jennings and Lashley ('13) give a formula for determining the most probable number of pairs that will be found to be alike in respect to any such character if the pairing has nothing to do with the distribution. This formula is:

$$k = \frac{(n + 1)\ (n/2 + 1)}{m + 3}$$

in which the nearest integer below k is the most probable number of pairs in which the two members will be found alike in the character in question; n is the number of cases (lines) in which this character occurs, while m is the total number of cases (lines of descent from exconjugants in this case). (This formula holds absolutely only when n is even, but by obtaining the result for the two even numbers above and below the actual number, if the latter is odd, the difficulty may be avoided.)

In examining this matter for our case with respect to normality and abnormality, 17 of the 131 pairs of the first experiment must be omitted from consideration, since in these the characteristics of one or both members is unknown. This leaves 114 pairs to be dealt with, giving 228 lines of descent. In the second experiment 3 of the 100 pairs must be omitted from consideration, leaving 97 pairs to be dealt with, giving 194 lines of descent. In the third experiment there are 14 pairs to be considered, giving 28 lines of descent. This makes 450 lines of descent all together.

Of these 225 pairs, in the first experiment both members in 48 gave normal lines, both members in 26 gave abnormal lines, while in 40 the two members gave lines diverse in this respect. The total number of normal individuals was therefore 136, of abnormal individuals 92. In the second experiment, both members in 7 gave normal lines, both members in 69 gave abnormal lines, while in 21 the two members gave lines diverse in this respect. The total number of normal individuals of experiment 2 was therefore 35; of abnormal individuals 159. In Experiment 3, both members in 8 pairs gave normal lines, and both members in 6 gave abnormal lines; pairing was perfect. The total number of normal lines of Experiment 3 was therefore 16; of abnormal lines, 12.

How many pairs with both lines abnormal should we expect to find in these cases if pairing does not affect the distribution of abnormalities? In the first experiment n is 92, while m is 228. Applying the formula we find that the expected number of pairs with both members abnormal is 18; the actual number is 28. In the second experiment n is 159 while m is 194. By the formula the expected number of pairs with both members abnormal is 66, while the actual number is 69. In the third experiment n is 12 while m is 28. The expected number of pairs is 2, the actual 6. In the same way the expected number of pairs with both members normal is in the first experiment 40, while the actual number is 48; in the second experiment the expected number is 3 the actual 7; in the third, the expected number is 4 the actual 8.

It is therefore clear that in all three experiments the number of like members of pairs is greater than would be the case if the pairing had no effect on the distribution of the abnormalities. *Conjugation tends to cause the descendants of the two members of pairs to become alike in respect to abnormality and normality.*

Some of the exconjugants never divided after separation. The same question may be examined with respect to them. Do the two members of a pair tend to have the same fate in this respect? There were 72 exconjugants that never divided, out of the 228 of the first experiment, and 27 out of the 194 of the second

experiment. In the first experiment both members in 19 pairs were affected; in the second experiment, both members in 8 pairs. Applying the formula (first experiment, $n = 72, m = 228$; second experiment, $n = 27$, $m = 194$) we find that if pairing has no effect on the matter, the most probable number of cases for both members in the first experiment is 11; in the second, 2. Similarly there are in the first experiment 61 pairs in which both members divided, while the most probable number is 53. In the second experiment the actual number is 79, the most probable is 72. Again we find that conjugation increases the resemblance of members of pairs in this respect.

It will be of interest also to give the relation of pairing to the date on which the lines finally died out. This is known for both members of but 51 pairs of the first experiment, and 41 of the second. The numbers in the third experiment are too small to be considered. In some cases the descendants of both members of a pair completely died out on the same date; in other cases the descendants of one member lived longer than those of the other.

The main facts are these. In the first experiment, on December 5, twenty lines were found to have died out; these included both members of 8 pairs. The probable number of pairs if conjugation does not affect the date of death is but 2. On December 7, 53 individual lines ended, including both members of 20 pairs. The most probable number of pairs would be but 14. On later dates the numbers are too small to be significant. In the second experiment on December 6, 31 lines were found to have died out; these included both members in 7 pairs. The probable number of pairs if pairing does not affect the date of death is but 6. On all the other dates the numbers were so small that they are not worth considering. Conjugation thus tends to make descendants of the two members of a pair alike in their length of life (in their 'vitality').

All together, the evidence shows that conjugation induces resemblances in the two members of a pair in respect to all the characters examined: in the tendency to fail to reproduce after conjugation; in the abnormalities produced by their offspring; and in the length of life of the stocks produced.

VII. SUMMARY AND DISCUSSION OF RESULTS

Among the progeny of a large proportion (from 36 to 81 per cent in the different experiments) of exconjugants of Paramecium caudatum, abnormalities appear frequently and constantly.

These abnormalities show themselves to be hereditary in the following respects:

1. Lines derived from different exconjugants differ in respect to them: some lines show no abnormalities; others show a small proportion of abnormal individuals; others large proportions up to cases in which abnormality is almost or quite universal. The tendency to abnormality is transmitted in fission; definite proportions of abnormality being characteristic of particular lines. In one case there was inheritance of a specific type of abnormality carried through 303 generations (Race C).

2. The diversities in abnormality occurring within a single line of descent (derived from a single exconjugant) are in some lines not hereditary, so far as can be determined by long continued selection. In a very large proportion of the races in which the abnormals were regularly discarded and only normals retained to carry on the race, the abnormal character persistently reappeared, the selected normals producing abnormal progeny. In all the abnormal races there is a wide variation in degree of abnormality of the individual, from those perfectly normal to the monsters so deformed that they would never be recognized as paramecia if their history were not known. Yet, as stated above, in most cases the progeny of all these variations were alike, the daughter cells of normal individuals being often just as abnormal, or even more so, than the daughter cells of monsters. This of course agrees with the conditions found in most of the studies on inheritance in 'pure lines' or clones: the diversities within the lines are not inherited.

3. But in other lines diversities within the line showed themselves to be heritable, so that selection gave very different results from those usually obtained in pure line work. By selection, single lines, derived by fission from a single parent, were divided into two or more races differing hereditarily. This was success-

fully accomplished in twenty-five races; from each of these were isolated two sorts of lines, one quite normal, the other continually producing abnormalities—the two cultivated side by side.

Calkins and Gregory ('13) have in some cases obtained four diverse races from the four primary daughter cells, or 'quadrants' of an exconjugant—these being the four individuals that receive the four macro-nuclei produced before fission occurs. It is to be noted that our selection resulting in the isolation of lines differing hereditarily in abnormality has often been brought about much later in the series of generations, so that the differentiation has occurred within the compass of a single 'quadrant,' or indeed within a much narrower fraction of the descent. In several cases differentiation through selection did not begin till after several weeks had passed with production of a great number of generations. Thus the results of selection in the present case cannot be interpreted as due to a primary difference in the four original macronuclei produced during conjugation. Selection is effective when begun with progeny of a single individual that has appeared many generations after conjugation.

4. In a race of Paramecium which upon extended examination shows no hereditary abnormalities, conjugation results in the appearance of many lines which are hereditarily abnormal, others which are normal throughout (Experiment 2).

This is of course an example of what Jennings ('13) has described as the 'production of variation by conjugation.' It appears to fully meet the desire of Dobell ('14, p. 172) for "convincing evidence of a concrete instance in which from a known race—constant in a certain character—a new race—permanently diverse in this character—has arisen as a result of conjugation." For in Experiment 2, from a clone with a constant character of normality (as shown by the progeny of the 54 split pairs of this clone) 101 races which were permanently diverse from the original one, being hereditarily abnormal, arose as a result of conjugation.

5. In the diverse lines descended from the different exconjugants of a conjugating culture, the two lines descended from the two individuals that have conjugated together tend to be

alike in respect to normality or abnormality. That is, if the progeny of the exconjugant *a* are abnormal, the progeny of its mate *b* are more frequently abnormal than would be the case if the distribution of abnormal races were not affected by conjugation. This is an example of what Jennings and Lashley ('13) have called biparental inheritance as a result of conjugation. As these authors point out and as Dobell ('14) has recently emphasized, this does not mean that the characters of the progeny of the two exconjugants are known to resemble the characters which the two parents had before they conjugated. It means merely that the characteristics of the progeny of *a* are not determined by the nature of *a* alone, but partly also by the fact that *a* has conjugated with *b*. Just what the resulting similarity of the progeny of *a* and *b* should be called is of little importance, as compared with a clear grasp of the facts in the case, yet it is perhaps worth while to point out that similar relations often appear in what is called inheritance in higher organisms. Two heterozygotic parents frequently produce progeny which differ from both of them, yet what the progeny shall be is determined by the constitution of both of the parents.

6. We are dealing here with characters that are called abnormal. What is the bearing of this on any conclusions drawn from this study? Can we learn anything worth while from the study of abnormal characters?

What we can learn from abnormalities, and what the relation of their behavior is to that of other characters can be determined only by investigation; the present paper is offered as a contribution toward answering such questions. But certain general principles appear worthy of consideration. What is the real status of the conception of abnormality? Does it mean anything more than that the condition so characterized is not the one usually found? It certainly does not mean that the condition is one not subject to law of any sort. If we characterize the course of inheritance of these characters as abnormal, we can mean no more than that they do not follow the usual course. But the course they do follow is one actually occurring in animals, and therefore one not inconsistent with the nature

of organic matter or the constitution of organisms. It is perfectly possible for organisms to exist in which hereditary variations occur during non-sexual reproduction, and in which these variations can be accumulated through selection; for in the characters here studied this does occur. No one therefore can say a priori what characters must descend in this manner, what in some other manner.

It is then an open question whether a similar scheme of descent may not be followed by other characters, either in this same organism, or in other organisms. Jollos ('14) has raised the question whether all the hereditary variations shown by Jennings to follow upon conjugation may not be of the nature of abnormalities. It is entirely possible that all show the same scheme of descent as the 'abnormalities' considered in this paper; but if so then the 'abnormal' cannot be characterized as the unusual. In the same way it is possible that the hereditary differences among the progeny of single exconjugants observed by Calkins and Gregory ('13) may be of the same nature as these abnormalities. It is quite possible that lines might be 'abnormal' in ways evident only through study of the fission rate, or the like. But with such a state of the case the distinction between abnormal and normal becomes evanescent.

The facts are, that in Paramecium as a result of conjugation, there appear lines or races that are hereditarily diverse; and that within some of these lines hereditary diversities likewise appear even during asexual multiplication. Whether we can maintain some special category such as 'abnormality' for all these cases, can be discussed; but this does not do away with the facts as to their existence and the scheme of their descent from generation to generation.

It is of interest to compare the genetics of these abnormalities in Paramecium with abnormalities in other organisms. Almost all the characters studied by Morgan and his associates in Drosophila, on which have been reached results of such immense importance for the entire theory of genetics, may be characterized as abnormalities. A large porportion of them show, as is well known, typical Mendelian inheritance. Others show a

more irregular course, resembling in this respect those of Paramecium. Such a character is the 'beaded wing,' recently studied by Dexter ('14). Lutz ('11) had previously investigated an abnormal wing character in Drosophila, with results that are still more similar to the conditions shown in Paramecium. Lutz found that certain abnormalities of venation were heritable, but, as in Paramecium, the inheritance was not precise; the abnormalities of parent and offspring might be diverse, but the tendency to produce some sort of abnormality of venation was inherited. Furthermore the proportion of individuals abnormal, and the degree of abnormality, were modifiable by selection, apparently through fine gradations. Lutz is of course working with bisexual reproduction, which greatly complicates the interpretation of the matter. Yet selection continued to be effective after ten generations of inbreeding, at which time it would be expected that a homozygotic strain would have been reached, if the character were dependent on typical Mendelian units.

In many other cases abnormalities have been shown to follow aberrant types of heredity; to attempt a general review of the matter here would lead too far.

VIII. LITERATURE

BALBIANI, E. G. 1893 Nouvelles recherches expérimentales sur la mérotomie des Infusoires ciliés. Ann. Microgr., Paris, 4.

BATESON, W. 1914 The Address of the President of the British Association for the Advancement of Science. Science, 40.

CALKINS, G. N. 1911 Effects produced by cutting Paramecium cells. Biol. Bull., 21.

and CULL, S. W. 1907 The Conjugation of Paramecium aurelia (caudatum). Arch. f. Protistenk., 10.

and GREGORY, L. H. 1913 Variations in the progeny of a single exconjugant of Paramecium caudatum. Jour. Exp. Zoöl., 15.

DEXTER, J. S. 1914 The analysis of a case of continuous variation in Drosophila by a study of its linkage relations. Amer. Nat., 43.

DOBELL, C. 1914 A commentary on the genetics of the ciliate Protozoa. Jour. of Gen., 4.

HERTWIG, R. 1908 Ueber neue Probleme der Zellenlehre. Arch. f. Zellforsch., 1.

JENNINGS, H. S. 1908 Heredity, variation, and evolution in Protozoa. I. The fate of new structural characters in Paramecium, etc. Jour. Exp. Zoöl., 5.

1913 The effect of conjugation in Paramecium. Jour. Exp. Zoöl., 14.

and LASHLEY, K. S. 1914 Biparental inheritance and the question of sexuality in Paramecium. Jour. Exp. Zoöl., 14.

1913 a Biparental inheritance of size in Paramecium. Jour. Exp. Zoöl., 15.

JOLLOS, V. 1913 Experimentelle Untersuchungen an Infusorien. (Vorl. Mitteil.) Biol. Centralb., 33.

1914 Variabilität und Vererbung bei Mikroorganismen. Zeitsch. f. Ind. Abst., 12.

LEWIN, K. R. 1910 Nuclear relations of Paramecium caudatum during the sexual period. Proc. Cambridge Phil. Soc., 16.

LUTZ, F. E. 1911 Experiments with Drosophila ampelophila concerning evolution. Carnegie Inst. Pub., 143.

MALL, F. P. 1908 A study of the causes underlying the origin of human monsters. Jour. of Morph., 19.

MCCLENDON, J. F. 1909 Protozoan studies. Journ. Exp. Zoöl., 6.

PEEBLES, F. 1912 Regeneration and regulation in Paramecium caudatum. Biol. Bull., 23.

POPOFF, M. 1908 Experimentelle Zellstudien. Arch. f. Zellforsch., 1.

1909 Experimentelle Zellstudien II. Ueber die Zellgrosse, ihre Fixierung and Vererbung. Arch. f. Zellforsch., 3.

RAUTMAN, H. 1909 Der Einfluss der Temperatur auf das Grossenverhältnis des Protoplasmakörpers zum Kern. Arch. f. Zellforsch., 3.

SIMPSON, J. Y. 1901 Observations on binary fission in the life history of Ciliata. Proc. Roy. Soc. Edinburgh, 23.

WOODRUFF, L. W. and ERDMANN, R. 1914 A normal periodic reorganization process without cell fusion in Paramecium. Jour. Exp. Zoöl., 17.

VITA

Ruth Jennings Stocking was born in Elyria, Ohio, March 31, 1887. She entered Goucher College in 1906 and graduated in 1910 with the degree of A.B. From October 1911 to June 1912 she was a graduate student in Biology and Physiology at Bryn Mawr College. From October 1910 to June 1911, and from October 1912 to June 1915 she has been a graduate student in Zoölogy, Psychology, and Botany at the Johns Hopkins University. She held the fellowship in Biology at Bryn Mawr College during the academic year 1911–1912; the Alice Freemen Palmer Research Fellowship of Wellesley College, 1913–1914, being in residence at the Johns Hopkins University; a University Scholarship, 1910–1911, a University Fellowship, 1912–1913, and a Fellowship by Courtesy, 1914–1915, at the Johns Hopkins University.

THE JOURNAL OF EXPERIMENTAL ZOÖLOGY,

VOLUME 19, NUMBER 4, NOVEMBER, 1915

CONTENTS

RUTH J. STOCKING. Variation and inheritance in abnormalities occurring after conjugation in Paramecium caudatum. Twenty figures..... 387

AUSTIN RALPH MIDDLETON. Heritable variations and the results of selection in the fission rate of Stylonychia pustulata. Seventeen figures..... 451

CHARLES ZELENY AND C. T. SENAY. Variation in head length of spermatozoa in seven additional species of insects. Eight figures..... 505

CHARLES ZELENY AND E. W. MATTOON. The effect of selection upon the 'bar eye' mutant of Drosophila. Five figures..... 515

MARY B. STARK. The occurrence of lethal factors in inbred and wild stocks of Drosophila. Two diagrams..... 531

JACQUES LOEB AND MARY MITCHELL CHAMBERLAIN. An attempt at a physico-chemical explanation of certain groups of fluctuating variation..... 559

THE WAVERLY PRESS
BALTIMORE, U. S. A.